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BIOLOGICAL BULLETIN

THE HABITS AND MOVEMENTS OF THE RAZOR-SHELL CLAM, ENSIS DIRECTUS, CON.

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Many of the older naturalists have called attention to the sensitiveness and remarkable activity of this form, and the consequent difficulty that is sometimes experienced in capturing it. Some of the observations are not strictly accurate but they have served to call attention to its adaptation for a burrowing life. Even the uncommon shape of the animal indicates this adaptation

The species under consideration is to be found more or less abundantly all along the eastern coast of the United States. It is best known on sandy flats from which most of the water flows at low tide, where specimens may be dug with spade or clam-hoe. In some localities, as in restricted areas around Woods Holl and North Falmouth, Massachusetts, where most of these observations were made, the animals are quite abundant, and in such places one may find the protruding posterior ends of the shells, or see the siphon openings of the undisturbed individuals. They readily take alarm and even a slight jarring of the mud of the bottom in their vicinity serves as a signal for them to instantly disappear. It is this sudden disappearance that has attracted wide attention, and has given the impression that the animals are exceptionally hard to capture (5 and 6).

The species is probably not restricted to very shallow water. Specimens are not often taken in a dredge, but the position that they occupy buried in the rather hard sand or mud of the bottom, makes their capture unlikely. Young specimens, from a millimeter to a centimeter in length have been taken in large numbers

near South Hapswell, Maine, in from ten to thitry feet of water, by means of a fine wire dredge. Supposedly where conditions are right for individuals to grow to a centimeter in length, larger ones would thrive also.

The usual position for undisturbed specimens is with the posterior ends of the shells protruding just above the surface of the mud. Sometimes specimens are found with several centimeters of their shells protruding, but this is not very common. Again all that indicates the presence of a specimen, may be the depression at the spot where the animal has disappeared. The most conspicuous parts of a specimen in its normal position are the siphons, the openings of which appear as nearly round apertures surrounded by tentacles (Fig. 5). Close observation is necessary to see such specimens, as the color of their siphons is almost exactly the same as the bottom where they occur.

Specimens that have their posterior ends protruding above the surface of the mud seem to be more common where the water has drained entirely away than where the flats are still covered with water. Shells are not uncommon on the flats and shores, but they are seldom found embedded in the position that the animals occupy during life. These observations are of especial interest in view of the fact that animals in aquaria quite universally push up out of the mud before they die. The heat of the sun on the bare mud flats is probably disturbing and may cause them to react in the same way they do before they die. If animals react in nature as they do in aquaria, it is natural that the shells of dead animals should be found on the surface.

Specimens are not easily studied in their native places because of ripples on the water and because the character of the bottom makes it hard to approach closely without disturbing them. Walking on the mud near them will cause them to withdraw their siphons or disappear beneath the surface. It has accordingly been more satisfactory to study specimens in aquaria that contain several inches of sand or mud from the bottom from which the specimens were obtained. The animals do not live well in aquaria, even when supplied with running water, but for several hours after they are collected, they remain very active and seem to be quite normal.

If a specimen is touched it will either withdraw its siphons anp

remain quiet until disturbed again, or it will immediately vanish beneath the surface of the mud. If a specimen is grasped and pulled upward there is an immediate response that is so powerful that the animal frequently escapes and disappears. This fact Tryon (6) mentions, saying: "It may often be seen at low tide projecting a little above the level of the sand but, if touched or disturbed, it descends with astonishing rapidity and force, much to the amazement of him who may lay hold of it thinking to make an easy capture." These observations indicate that the animal probably habitually keeps its foot protruded some distance out of the shell to be ready for disturbances.

Specimens taken in firm sandy soil, where the depth can be noted, are frequently found several inches below the surface. Verrill and Smith (7) report that this species digs somewhat permanent burrows that extend nearly perpendicularly into the sand to the depth of three feet, and Woodward (8) states that the animals never voluntarily leave their burrows. I have never been able to demonstrate permanent burrows in the localities where I have worked, but the usual muddy character of the bottom was not satisfactory for the purpose. I doubt, however, if such burrows are habitually constructed. The character of the bottom where they live is frequently not suitable for permanent burrows unless something like a tough secretion is added to the mud to keep it in place, and such a secretion does not seem to be formed. Specimens in aquaria never seem to construct anything like permanent burrows.

As individuals are known to burrow to some depth it is probable that in digging for them, those in the immediate vicinity are disturbed and burrow beneath the reach of the shovel. Verrill and Smith (7) call attention to how easily disturbed they are and say: "When thus alarmed it is generally useless to try to dig them out, for they quickly descend beyond the reach of the spade." Dr. J. Gwynn Jeffreys as quoted by Tryon (6) reports them as having exceptional powers for detecting disturbances. He says: "They are evidently sensible to vibratory movements in the air, as well as on ground, taking alarm at greater or less distances according to the state of the atmosphere and the direction of the wind." It is hard to verify these observations and I am inclined to think they are not accurate, but there can be no

doubt that specimens are easily disturbed by vibrations of the bottom. That they habitually burrow to some depth is indicated by the fact that after the first half dozen trials, specimens are not usually obtained without going to another spot several feet away, although the first trials may have resulted in one or more specimens each.

When dug from the mud, individuals frequently leap or swim. In leaping the shell may be thrown several inches by the action of the foot. In swimming the animal progresses posterior end first and large specimens may swim several feet before stopping. The foot is always active while the animal is swimming. These activities, together with the movements of burrowing, will receive attention later.

Before describing the movements it is desirable to call attention to some points of anatomy.

The shell is of nearly even diameter both dorso-ventrally and laterally (Figs. 1 and 4), throughout its length, except very near its ends. Anteriorly it contracts in both directions a little, but the anterior margins of the shell valves remain wide apart even when they are in contact along their ventral borders (Fig. 6). This leaves ample space for the protrusion or withdrawal of the foot when the shell is closed. The anterior margins of the lobes of the mantle are thickened and extended, so, when the foot is withdrawn into the shell, these flaps cover the opening between the shell valves (Fig. 6). When the foot is extended the flaps are spread apart and form a collar around the foot, the free margins of which are in contact with the foot (Figs. 1 and 4). The collar is thick and muscular, being well supplied with the radial pallial muscles, and as it is held tightly against the foot, forms a very effective scraper, that cleans the foot so mud is not drawn into the shell with it. The cilia covering the foot no doubt aid in loosing the mud so it is easily scraped off. The flexible collar adapts itself to the shape of the foot so its margin is applied to the surface of the foot until its very extremity is drawn into the shell (Figs. 6 and 7).

The posterior end of the shell narrows laterally, but here again the margins of the shell valves are wide apart when the ventral edges of the valves are in contact (Fig. 5). This makes it possible for the siphons to be at least partially extended when the

shell is closed. The reason for this arrangement is found by studying the movements of burrowing and swimming.

The siphons have nearly circular or slightly elliptical openings, and are separated near their extremities. The whole posterior end of the mantle, bearing the siphons, may be protruded some distance beyond the posterior end of the shell. Sense tentacles surround the siphons near their bases and occur on the mantle dorsally and ventrally near the posterior end, where the mantle is exposed between the shell valves (Figs. 2 and 5). Small sense tentacles occur on the surfaces of both siphons, and the branchial siphon bears a number along its extremity that tend to radiate in over the opening of this siphon. The margin of the cloacal siphon has no tentacles. Verrill and Smith have (7) described a definite arrangement for the tentacles but it is doubtful if this arrangement always holds.

The ventral margins of the mantle lobes are united throughout their length except near the middle of the length of the animal, where a small opening remains that is situated just posterior to the retracted foot (Fig. 4). This opening is surrounded by a single row of sense tentacles. Except for this opening, the opening through which the foot is protruded, and the openings of the siphons, the mantle forms a closed chamber.

The united mantle margins are very muscular, being provided with strong circular and radial pallial muscles that are very similar to the muscles of the mantle margins in *Solenomya* (2) where they serve very much the same purpose, that is, to close the shell tightly and to obliterate a portion of the mantle chamber. Like *Solenomya* the valves of the shell are covered with a very heavy, elastic cuticle that is extended beyond the calcareous margins. Mud does not readily adhere to this cuticle. When the valves are closed the cuticle is bent in over the hard margins of the shell (Fig. 8), thus allowing the united margins of the mantle to be withdrawn. Probably this elastic cuticle aids in opening the mantle chamber when the muscles relax, as is undoubtedly the case with *Solenomya* (2), but the effect in this form is certainly much less than in *Solenomya*.

Both adductor muscles are present. The anterior adductor is very large and strong. The posterior adductor is quite small and does not seem to function actively. The united margins of

the mantle posterior to the ventral opening are especially muscular and seem to replace the posterior adductor in function to a marked extent.

The foot, when retracted into the shell, is nearly cylindrical and together with other organs completely fills the part anterior to the ventral opening in the mantle. The dorsal portion of its extremity is pointed, and a slight ridge marks the boundary of what may be called the sole (Fig. 2). The foot is very powerful and remarkably active, its movements being very unlike the slow movements of the foot in most lamellibranchs. It may be thrust from the anterior end of the shell to a distance exceeding one half the length of the shell, and in this position the end may be swelled into a knob or bulb that considerably exceeds the diameter of the shell (Fig. 1). The knob is not cylindrical but is extended dorso-ventrally and laterally and the free extremity or sole is comparatively flattened. In this swollen condition the end of the foot forms a very efficient anchor, as will be found by grasping a shell and trying to withdraw it from the mud. The resistance of the expanded foot is so great that the foot is frequently torn away from the shell when the shell is jerked quickly (7). The foot is attached to the shell by two pairs of foot muscles, both of which are strong and aid in withdrawing the foot into the shell. With the end of the foot anchored, the obvious result of the contraction of these muscles is to pull the shell into the mud up to the position of the bulbous portion of the foot.

For our present purpose it is not necessary to give more attention to the anatomy of the animal, and we will proceed at once to the study of the movements.

Burrowing. — The movements of burrowing may be best studied either in specimens placed in shallow dishes of sea water, which are very likely to execute the movements soon after they are placed in the water, or in specimens held with the anterior end pointing downward and stimulated to activity by stroking the sense tentacles around the ventral opening in the mantle and around the siphons. Specimens in the water are more normal in their movements than the specimens held and stimulated as described. Apparently the action of gravity may cause the held specimen to protrude its foot and to partially expand the end of

it, in which position the foot may remain quiet for some time. When the movements are active they are essentially the same in both cases. The foot is slowly protruded with the pointed tip working as if trying to bore into the mud, ending each time with a dorsal thrust. These movements are continued until the foot is fully extended. During this extension the end of the foot is kept small, the point is directed well forward, and the general diameter of the protruded part of the foot is decidedly less than its normal diameter when at rest. When the foot reaches its greatest extension, the end is suddenly swelled into a great bulb, more than twice the diameter of the remainder of the foot (Figs. 1 and 4) and the whole foot becomes very rigid. That this result is attained by injecting blood into the foot may be readily proved by sticking spring forceps into the end of the foot so the spring will hold the wound open, and stimulating the foot to activity by stroking the tentacles as before described. When the foot starts to become active the wound begins to bleed rapidly, and when the final effort to swell the end of the foot is made, the blood rushes out in a great jet, but the swelling is slight. A simple incision does not answer as well, as the contracting muscles seem to close the wound more or less perfectly.

The instant that the swelling of the end of the foot is complete, a process that takes place so rapidly as to be almost startling, the retractor muscles pull the foot back to the shell with a jerk, the end remaining swollen until it reaches the shell (Fig. 7). It is then reduced in size and either withdrawn into the shell or extended in the beginning of a new burrowing movement.

While the foot is being extended the shell valves are allowed to gap apart and the siphons and ventral opening in the mantle are kept more or less widely open. Just before the final sudden retraction, the siphons and ventral opening are all tightly closed, and kept so until retraction is complete. The result is that the water in the mantle chamber is discharged through the opening through which the foot is extended, between the collar and the foot. Whether the water escapes all around the foot or only ventral to it, where the contact of the collar is poorest, has not been determined, but the jet of water is quite powerful. When the shell is embedded in the mud, each retraction of the foot,

squirts the water against the mud ahead of the shell, the shell is decreased in diameter by being closed, and the mud is dislodged and washed up the sides of the shell where it may be seen raising after each downward movement of the shell. The action is similar to the pile driver that opens a way for the pile by a somewhat similar stream of water.

The burrowing movements may follow each other quite rapidly but the extension of the foot is never very rapid, as it must be carefully worked into the mud to keep from forcing the shell back. The opening of the shell just before the extension of the foot, tends to embed it more firmly and thus to hold it in position while the foot is being worked into the mud.

A specimen laid on its side on mud, has no difficulty in gaining a hold with its foot that enables it to right itself and start the anterior end into the mud. Burrowing is then normal, and the shell is soon completely buried. The time necessary for a specimen to completely bury itself varies with the character of the mud. In soft mud the thrusts may be rapid and few are needed, in hard sand the thrusts will necessarily be slower and more movements are required, but even in such material the animal will disappear very promptly. When the animal is laid on its side on such sandy mud as that in which it usually lives, one movement will frequently suffice for it to right itself, and four or five more will carry it out of sight. The time necessary for this may be less than half a minute. Embedded as the animal usually lives, a single retraction takes it out of sight and away from enemies.

Swimming. — It is more difficult to study the movements of swimming, as animals swim only occasionally, and then generally immediately after being dug, and the movements of parts of the animal, and the animal as a whole, are so rapid as to make accurate observations difficult. The following points have been determined however and, from these, conclusions may be drawn: (1) The animal progresses posterior end foremost; (2) movements are by jerks, each jerk carrying the animal one or more times its length; (3) the foot is very active, being thrust out and withdrawn repeatedly. The outward thrust is comparatively slow but the withdrawal is extremely rapid; (4) apparently the valves of the shell are drawn together every time the foot is re-

tracted; (5) each movement of the animal as a whole, corresponds to the period of retraction of the foot.

In describing the movements of burrowing it has already been mentioned that water is thrown from the shell, through the opening through which the foot is protruded, every time the foot is retracted into the shell. Each jet is caused by closing the other openings into the mantle chamber and driving the water out by pulling the foot in, by closing the shell by the contraction of the adductor muscles and the united margins of the lobes of the mantle, and by drawing the mantle margins, with the shell cuticle to which they are attached, into the mantle chamber (Fig. 8). The resultant action is to drive out most of the water that was between the valves of the shell, as nearly all of the space is now occupied by organs of the body. As all of the openings except the one around the foot are held closed, a very strong jet of water must be forced out around the sides of the foot. This is sufficient to cause the movement of the animal in the opposite direction. Many muscles, all of which are powerful, are used in this action, and as the water is thrown through a small opening between the muscular collar and the foot, the resulting force is considerable. The action, so far as movement is concerned, is similiar to what is so well known in the squid, and differs from the movement of *Solenomya* only in direction (2). Here the movement is posterior, in *Solenomya* the movement is anterior. Here the water is admitted through the siphons, and possibly also around the foot, and then, with the siphons closed, the water is thrown from the anterior end of the animal. In *Solenomya* the water is admitted around the foot, which opening is then closed and the water is thrown through the posterior opening. The method of forming the jet is quite the same in both animals. In both forms the same organs are used, but in *Solenomya* more use is made of the mantle margins and less of the retraction of the foot than is the case in this form.

Throwing strong jets of water from the siphons must aid lamellibranchs in keeping their mantle chambers clean. Some forms need to throw more powerful jets than others because the conditions under which they live demand it. A diversion of this use is apparently to be seen in the forms that swim either by

clapping the shell valves together, as in the case of *Pecten* (3), or by the more complicated method used by *Solenomya* and the form under consideration. It is likely that the jets thrown by this form are of very secondary importance, so far as swimming is concerned, and that their chief function is to aid the animal in burrowing. This is indicated by the fact that the jets are thrown from the anterior end of the shell, while in forms that use them for cleaning the mantle chamber only, they are thrown from the siphons.

Leaping. — Leaping may consist simply of a sudden, powerful protrusion of the foot, in which case the animal generally turns so as to lie somewhat nearly on its dorsal margin and catches the tip of its foot in the mud as it is protruded. The shell is thus thrown posteriorly. Generally, however, the foot is bent back under the shell, which is turned partly over towards its dorsal margin (Fig. 3) and is then suddenly made rigid with the result that it straightens out with great rapidity. This may result in projecting the animal backward, or in certain cases the foot may catch so as to turn the shell more or less completely end for end. Leaping movements are usually rapidly repeated several times when they are once begun. In many ways they resemble similar movements in *Yoldia* and *Solenomya* (2), but the foot of this form is so much longer that the impression of much greater activity is left with the observer.

The perfection of the movements of burrowing by a form that lives in the mud, so it may be able to escape its enemies, is of so much importance as to need no comment. When combined with sense organs that give immediate information of the presence of enemies, and with protective coloration that hides it from its enemies until they shall have given it warning, the rapid burrowing movements form a striking adaptation.

The uses of the swimming and leaping movements are not quite so evident. Small razor-shell clams have been taken in tow nets at the surface of the sea. The ability to swim is, then, sufficient to make it possible for the young specimens, at least, to change their positions after settling to the bottom, and after the larval locomotor organ, the velum, has been lost. If the first location does not offer the necessary food or bottom conditions, it is pos-

sible to move. Although the machinery for this is rather clumsy, and was primarily designed for another purpose, that of burrowing, it might be the deciding factor in the struggle of life. The fact that young specimens may be taken at the surface of the water, even the fact that the animals are able to swim at all, indicates that they probably occasionally change their positions. The statement made by Woodward (8) that the animals never voluntarily leave their burrows seems doubtful. They certainly do leave the mud when they are about to die, and there is no reason to believe that they might not voluntarily move from one place to another should occasion require.

Leaping may aid the animals in getting free from certain kinds of bottom or even occasionally in escaping enemies, should they be removed from the mud in any manner. Not infrequently specimens that have been swimming might become lodged so they could not burrow without changing their positions, and then the leaping movements would be of advantage.

Summary.

The animal is very active, burrows with great rapidity, and may also swim and leap.

In burrowing, the foot is worked into the mud as it is protruded, the end is then swelled into a knob, and by its sudden withdrawal the shell is drawn to the position of the anchored end of the foot. Simultaneous with the retraction of the foot, a strong jet of water is thrown from the anterior end of the shell, so the mud is softened or even washed away as the shell descends, an action similar to that of some of the modern pile drivers. A collar, formed by the anterior end of the mantle, surrounds the foot and acts as a scraper that prevents mud from being drawn into the shell with the foot.

The animal is able to swim by throwing jets of water from the anterior end of the shell, thus progressing backward by a series of jerks.

By the uncommon activity of the foot the animal is able to throw itself about on the bottom.

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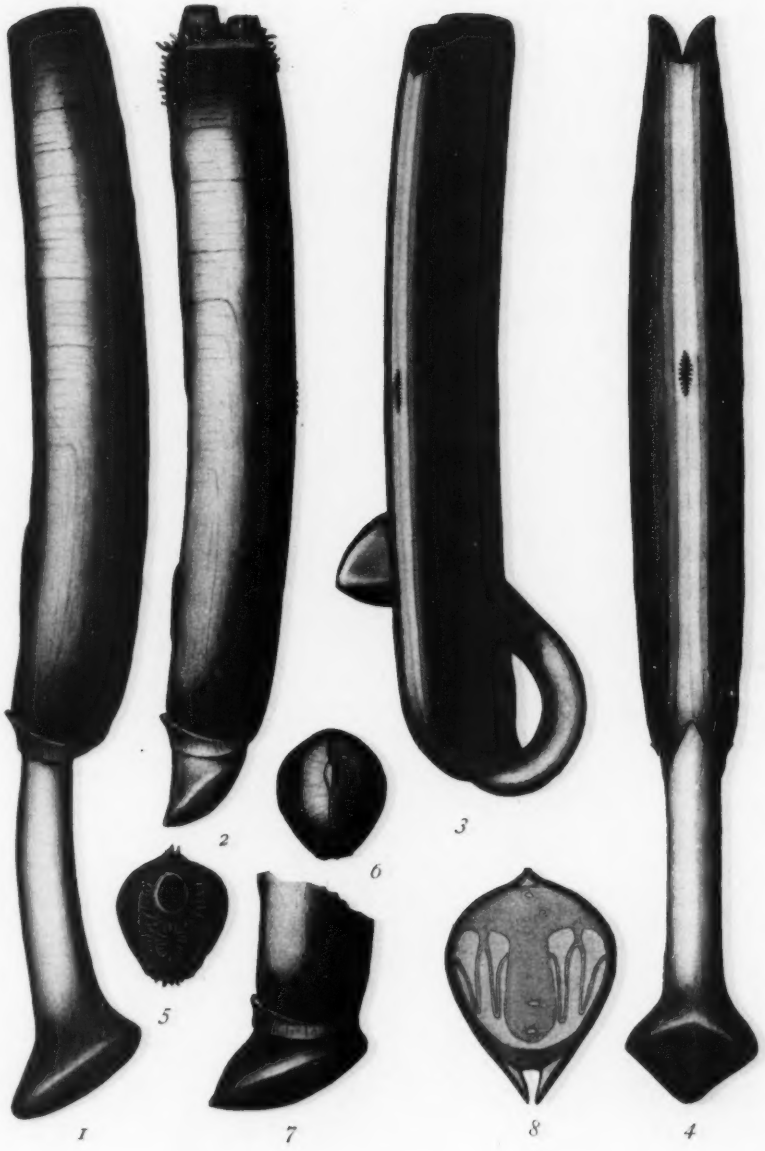
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Explanation of Plate II.

Fig. 1. A specimen with the foot extended and the end of the foot swelled, the instant previous to withdrawal. Drawn with the aid of an instantaneous photograph made by Mr. J. G. Hubbard of a specimen held with the anterior end down, and stimulated into activity. Natural size.

Fig. 2. A specimen showing the usual position assumed in a dish of sea-water. The siphons may be extended more than is shown in this figure. Drawn from observations. Natural size.

Fig. 3. A specimen showing the position assumed just before leaping. Drawn from observations. Natural size.

Fig. 4. Ventral view of a specimen that has the foot extended to the position shown in Fig. 1. Drawn from observations. Natural size.

Fig. 5. Direct view of the posterior end of an animal that has the siphons extended. Drawn from observations. Natural size.

Fig. 6. Direct view of the anterior end of a specimen that had withdrawn all but the tip of the foot, showing the adjustment of the collar. Drawn from observations. Natural size.

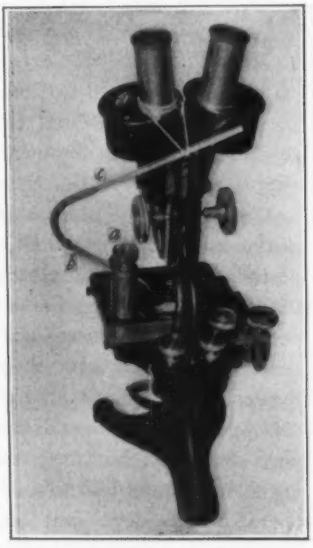
Fig. 7. Anterior end of a specimen showing the position and shape of the foot at the end of a burrowing movement. Drawn from observations. Natural size.

Fig. 8. Diagrammatic cross section of an animal, taken just posterior to the ventral opening in the mantle, to show how the mantle chamber is diminished by the contraction of the united mantle margins. Twice natural size.

EXPERIMENTS ON THE EGGS OF CHÆTOPTERUS AND ASTERIAS IN WHICH THE CHROMATIN WAS REMOVED.

J. F. McCLENDON.

Last July and August, while in the U. S. Bureau of Fisheries Laboratory at Wood's Hole, Mass., I devised an apparatus for removing blastomeres from ascidian eggs, but as the chorion of these eggs was too tough for a successful operation, I tried to use the apparatus for other purposes. I found that with it I could remove parts of the unsegmented eggs of echinoderms and annelids, and, in the few weeks at my disposal, performed the experiments mentioned below.



The Apparatus.

To a Greenough binocular stand (see accompanying figure) I attached a Spencer mechanical stage supplied with a fine adjustment screw (*a*) made by Wieback and Pietzsch, Philadelphia. The addition of this screw allowed movement in three dimensions, and the fine adjustment (*a*) carried a tube (*b*) drawn to a capillary opening at the lower end, and with the upper end attached by a rubber tube to the glass tube (*c*), which I held in my mouth during the operation. The lenses used were Zeiss binocular objective a_3 and a pair of Zeiss orthomorphic oculars, 4, giving a magnification of 65 diameters. Eggs were placed in 2–3 mm. depth of sea water in a glass dish on the stage of the microscope and the capillary end of the tube (*b*) inserted into the water above

them and allowed to remain until the water rose in it as high as it would by capillarity. The dish was moved until an egg of the most favorable orientation was brought in the center of the field. The capillary tube was then brought against the proper spot on the egg and a portion of the egg sucked away through the tube (*c*) which was held in the mouth. Immediately the operated egg was lifted from the dish by means of a capillary pipette just large enough to admit it easily, and placed in a watch glass half full of sea water. This capillary pipette does not need a bulb, as water enters it by capillarity. The size of the capillary end of the tube (*b*) was determined for the egg of each species by trial Some parts of the mechanical stage were an unnecessary hindrance and were removed.

Experiments on the Eggs of Chætopterus Pergamentaceus Cuvier.

Mead ('98[2]) and J. Loeb ('01) found that differentiation went on in the unfertilized egg of *Chætopterus* in solutions of KCl, and F. R. Lillie showed that this differentiation bears a semblance to the normal development save that cell division is usually suppressed.

I removed the chromosomes during the maturation divisions of the unfertilized egg in KCl solutions by sucking away the part of the egg immediately under the first polar body, in order to determine the effect of the chromatin on differentiation. A small percentage of eggs were so injured by the operation that they remained inactive until disintegration. Others, however, performed those "amœboid" movements which Loeb mistook for cleavage, just as in operated eggs. Further than this no changes were visible externally, but sections showed that irregular flowing of substances had taken place within the egg. None of the operated eggs developed cilia, and we might conclude that the chromatin is necessary for the formation of cilia, a function that has been attributed to the archoplasm. But as the centrosomes were probably removed with the chromosomes, and as the element of injury could not be excluded, this negative evidence should not be considered conclusive. Nearly one hundred eggs were operated on, and, although I do not think it advisable to

record the individual experiments, I will state the precautions against error that were used:

The majority of the *Chætopterus* females were gathered by me, or under my direct supervision, and were never placed in the same vessel with males. Each female was washed in a stream of fresh water before eggs were removed from it. Except during two days no males were allowed in the same laboratory with the females. One check of eggs in sea-water and another in sea-water to which KCl had been added, were kept to each experiment. None in the check in plain sea-water developed, while many in the KCl sea-water developed cilia. In each lot of eggs the operations were continued from the first appearance of the first polar body to the formation of the second polar body, and sometimes a few minutes later. Some eggs were fixed and sectioned immediately after the operation, others at later intervals up to twenty-four hours, and in this way was determined whether any chromatin had been left in the egg.

Experiments on the Eggs of Asterias Forbesii.

Eggs from which the chromosomes were removed and eggs from which the whole nucleus was removed were fertilized with sperm of the same species. These operated eggs did not show any differences from the normal save in number of chromosomes, in increased tendency toward polyspermy and in increased mortality. This last prevented my ascertaining whether any differences would appear in the later development.

An attempt was made to remove some of the chromosomes during the first cleavage, but the spindle was so much more viscid than the surrounding yolk that no part of it could be sucked out without removing all of it. In some sections the spindle was shown pulled to the surface of the egg but not very much distorted.

Eggs from which chromosomes were removed were mixed with sperm of a species of *Synapta*, but did not show signs of development save for the separation of the "fertilization membrane" from the egg.

In the experiments on the *Asterias* egg the following precautions were used: The starfish were washed in a strong stream of

fresh water before removal of the sexual organs, and after a male had been opened my instruments and hands were washed in like manner, to remove all spermatozoa. A check of unfertilized eggs was always kept, and in case some eggs developed in the check, the material was thrown out. In a number of experiments the eggs were fixed and sectioned as a further check.

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THE CONUS ARTERIOSUS IN TARPON ATLANTICUS (CUVIER & VALENCIENNES).

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The tubular prolongation of the arterial end of the heart furnished with numerous valves, and known as the conus arteriosus, is one of the characteristic features of elasmobranchs and ganoids. In *Amia calva*, the conus arteriosus is relatively shorter than in other ganoids, and its valves are reduced to three transversely arranged tiers. It may be said that the absence of the conus arteriosus as a separate structure is a characteristic of the teleostean heart, and that this fact is emphasized by a few recorded exceptions, all of which occur in teleostean families more or less closely related to *Amia*.

Among these exceptional teleosts only one has been hitherto described, which possesses more than one tier of conus valves, this is *Butirinus* (*Albula*) which has two, and to it may now be added *Tarpon atlanticus*.

The heart from which the following description is taken, was sent to me by Mr. Charles H. Townsend, director of the New York Aquarium. It comes from a specimen 5 feet 4 inches in length.[1] I take this opportunity of thanking Mr. Townsend for his courtesy in sending this heart, also an entire *Tarpon*, 4 feet 4 inches long, the heart of which is shown in Fig. 3.

The conus of *Tarpon atlanticus* resembles that of *Amia calva* in form, but differs from it in being proportionately smaller, in having two tiers of valves instead of three, and in appearing to have been driven into the heart towards the apex, so that, instead of projecting freely from the ventricle, as in *Amia*, it is more or less buried in the latter.

In the natural position, the conus of *Tarpon* is a horizontally placed longitudinal tube, elliptical in transverse section. The longest diameter of the ellipse is dorso-ventral, and measures 16

[1] Measurements include caudal fin.

mm., the shortest measures 11 mm., and is transverse. The conus wall is slightly under 2 mm. in thickness. The total length of the conus varies according to the site of measurement, at the mid-dorsal and mid-ventral lines it measures 8 mm., laterally its measurement increases, until at the mid-lateral line on either side it becomes 10 mm.

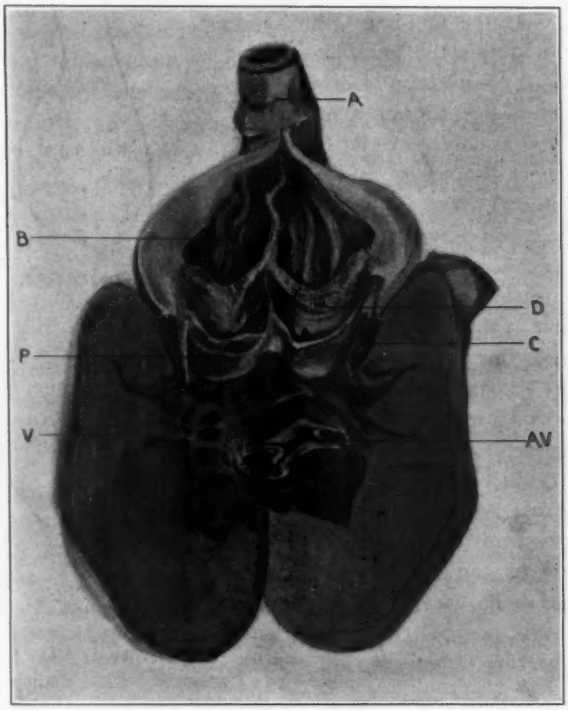

FIG. 1. The heart has been opened by a mid-ventral sagittal incision, and the parts widely separated (natural size). *A*, aorta; *AV*, atrio-ventricular valve; *B*, bulbus arteriosus; *C*, conus arteriosus; *D*, left distal conus valve; *P*, right proximal conus valve; *V*, wall of ventricle.

In order to compare the relative lengths of conus and ventricle in *Tarpon* and *Amia*, the length of the ventricle has been measured by plunging a needle into the apex of the ventricle, in such a direction that its point emerges where the ventricle and conus

blend. In this particular *Tarpon*, the ventricle thus measured is 41 mm. long, and taking 9 mm. as the average length of the conus, the proportion of the conus length to ventricle length, becomes 1 to 4.5. Six *Amia* hearts measured in the same way yield an average proportion of conus to ventricle of 1 to 1.76.

The exterior of the conus presents relations which differ in different regions. At the mid-lateral line, and ventral to this, the ventricle covers the conus completely. Dorsal to the mid-lateral line, the ventricle recedes rapidly, so as only to overlap the conus for a short distance on either side; in the interval, the conus is incompletely covered by the atrium. The area uncovered by ventricle and atrium measured back from the bulbus, is about 3 mm. in the midline, and lateral to this about 4 mm., it is covered by visceral pericardium. (These relations are indicated in Fig. 2.)

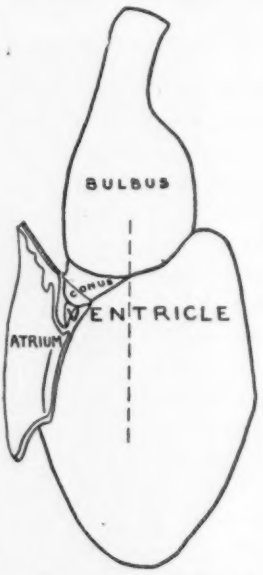

FIG. 2. Diagrammatic right lateral surface-view of bulbus, conus and ventricle. The atrium is represented as incised mesially, and the right half removed (natural size). The line across the conus indicates the site of reflection of visceral pericardium on to the atrium. The broken line indicates the site section in Fig. 3.

The conus is everywhere overlaid by a distinct layer of loose connective tissue, which separates it from the structures which cover it, and renders its outline very distinct in sections of the heart. Owing to the looseness of its connection with neighboring structures, the entire conus is easily exposed from the outside by incising the pericardium at the base of the bulbus, and stripping it away from the adjacent parts of the ventricle and atrium.

The conus valves are disposed in two transverse rows. Each row consists of a right and left cusp symmetrically placed with regard to the median dorso-ventral plane of the conus. Seen rom the lumen of the heart (as in Fig. 1) the valve cusps of

the proximal[1] and distal[1] rows appear to be approximately equal in size, this however is far from being the case, those of the distal row having a capacity far exceeding that of the proximal. The proximal valves are extremely fleshy at their attached margins, and shade rapidly into a thin semilunar area near the free edge; the edge itself is marked by a cord-like thickening, and is quite unattached, except at either end, where, having blended with the corresponding extremity of the other cusp, it is attached dorsally and ventrally to the mid-line of the bulbus a short distance beyond the conus.

The distal valves are not so fleshy as the proximal, and the marginal semilunar area is very thin and profusely perforated. The margins are free except at their extremities, the dorsal ends of the right and left valves blend at the mid-longitudinal region of the bulbus, and become continuous with an elastic cord, the other end of which is attached to the dorsal bulbus wall at its distal extremity. The ventral extremities of the distal valves blend at their point of attachment in the mid-line at the junction of the proximal and middle thirds of the ventral bulbus wall.

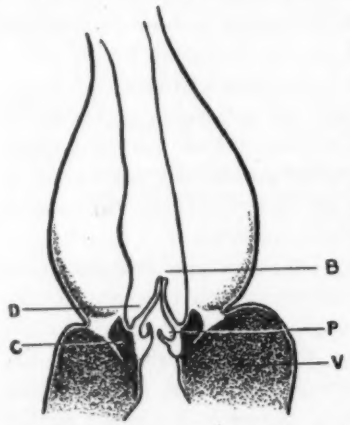

FIG. 3. Ventral face of a frontal section of the heart from the smaller, *Tarpon* its approximate source is indicated by the broken line in Fig. 3 ($\times \frac{1}{3}$). *B*, lumen of bulbus arteriosus; *C*, conus arteriosus; *D*, cavity of right distal conus valve; *P*, cavity of left proximal conus valve; *V*, wall of ventricle.

That the capacity of the distal valves is much greater than that of the proximal, is shown by the fact that a probe can be passed 11 mm. into the former, and only 3 mm. into the latter. To illustrate this point, a frontal section passing approximately through the mid-lateral line of another heart is shown in Fig. 3.

[1] The terms proximal and distal are used with regard to the ventricle.

The conus in *Tarpon* appears to differ from that of *Butirinus* (*Albula*) described by Boas ('80) in that it is less overlapped by the bulbus arteriosus, and more deeply buried in the ventricle, also in that it shows no diminution in length dorsally, as compared to the ventral measurement. The two subsidiary valves between the larger ones of the proximal row in *Albula* do not occur in *Tarpon*.

The sinu-atrial valves are two, with strong tensor muscles. There are four atrio-ventricular valves of which two are of large size, and two somewhat smaller. The hepatic vein, at its junction with the sinus venosus, is of almost cartilaginous rigidity, the size of the orifice is reduced by a thin fold of intima on either side, these almost meet mesially to convert the circular orifice into a vertical slit. The folds of intima appear to have no valvular action.

It is singular that since the appearance of Stannius's paper ('46) *Albula* should have enjoyed the reputation of being the only teleost provided with a conus having two rows of valves; whether the heart of *Megalops cyprinoides* will also prove to have more than one row of valves is an open question. So far as I am aware a description has not been recorded.

Of the other fishes showing evidence of near relationship to *Amia* the following have been examined with a negative result: *Elops saurus* by J. Mueller ('46), *Hyodon* by Mueller ('46) and Boas ('80), *Osteoglossum* by Mueller ('46) and Boas ('80), *Notopterus* by Boas ('80), *Mormyrops* by Mueller ('46). I have also examined *Elops saurus* (for a specimen of which I hereby beg to thank the authorities of the U. S. National Museum) *Hyodon tergisus* and *Notopterus borniensis*.

The original opinion of Gegenbaur ('66) which has been restated and amplified by Hoyer ('00) that the conus, although it has ceased to exist as a separate structure in the ordinary teleost heart, is represented by the portion of the myocardium adjacent to the aortic valves, is well illustrated by the conus relations in *Tarpon*. One has only to imagine the connective tissue layer between the exterior of the conus and the ventricle to have disappeared, allowing the conus muscle to be merged into the general myocardium, and the transition is complete; the relation of the myo-

cardium to the distal valve will be similar to that generally found in teleosts. An interesting transitional stage can be seen in the heart of *Dorosoma cepedianum*, where there is an extremely thin but distinct streak of connective tissue projecting into the myocardium for sufficient distance to clearly separate the areas of original conus and original ventricle.

PHILADELPHIA,
October, 1906.

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SOME SILKWORM MOTH REFLEXES.

VERNON L. KELLOGG.

Silkworm moths, *Bombyx mori*, are sexually mature and eager to mate immediately on issuing from the pupal cocoon. They take no food (their mouth parts are atrophied), they do not fly, they are unresponsive to light; their whole behavior, in fact, is determined by their response to the mating and egg-laying instincts. We have thus an animal of considerable complexity of organization, belonging to a group of organisms well advanced in the animal scale, in a most simple state for experimentation.

The female moth, nearly immobile, protrudes a paired scent-organ from the hindmost abdominal segment, and the male, walking nervously about and fluttering its useless wings, soon finds the female by virtue of its chemotactic response to the emanating odor. Males find the females exclusively by this response, but orient themselves for copulation (after reaching the female) by contact. When two males accidentally come into contact in their moving about they try persistently to copulate.

A male with antennæ intact, but with eyes blackened, finds females immediately and with just as much precision as those with eyes unblackened. A male with antennæ off and eyes unblackened does not find females unless by accident in its aimless moving about. But if a male with antennæ off does come into contact, by chance, with a female it always (or nearly so) readily and immediately mates. The male is not excited before touching the female, but is immediately and strongly so after coming in contact with her. Males with antennæ on become strongly excited when a female is brought within several inches of them.

The protruded scent-glands of the female are withdrawn into the body immediately on her being touched by a male. If the scent-glands are cut off and put wholly apart from the female, males are as strongly attracted to these isolated scent-glands as they are to unmutilated females; on the contrary they are not at all attracted to the mutilated females. If the cut-out scent-glands are put by the side of and but a little apart from the

female from which they are taken, the males always neglect the near-by live female and go directly to the scent-glands. Males attracted to the isolated scent-glands remain by them persistently trying to copulate with them, moving excitedly around and around them and over and over them with the external genitalia vainly trying to seize them.

The behavior of males with the antenna of only one side removed is striking. A male with left antenna off when within three or four inches of a female (with protruded scent-glands) becomes strongly excited and moves energetically around in repeated circles to the right, or rather in a flat spiral thus getting (usually) gradually nearer and nearer the female and finally coming into contact with her, when he is immediately controlled by the contact stimulus. A male with right antenna off circles or spirals to the left. It is a curious sight to see two males with right and left antenna off, respectively, circling violently about in opposite directions when the immobile female a few inches removed protrudes her scent-glands. This behavior is quite in accordance with Loeb's explanation of the forward movement of bilaterally symmetrical animals.

The results of all the experiments tried show how rigorously the male moths are controlled by the scent attraction (chemotropism) and how absolutely dependent mating (the one adult performance of the males) is on this reaction. If we can find specialized animals in a condition where all attractions and repulsions (stimuli) but one are eliminated we may readily perceive the rigorous control exercised by this remaining one. We are, unfortunately, in the general circumstances of animal life too much limited to the use of very simply organized animals for reaction and reflex experimentation. This tends to make it difficult to carry over to the behavior of complexly organized animals the physico-chemical interpretation which is steadily gaining ground as the key to the understanding of the springs and character of the behavior of the simplest organisms. But where the complex stimuli and reactions that determine the behavior of complexly organized forms can be isolated and studied the inevitableness of much of this behavior can be recognized.

Reflexes of Moths Without Cephalic and Thoracic Ganglia.—

A number of experiments was made to determine the need, or absence of need, of the principal ganglia of the central nervous system in the performance of the two chief reflexes in the silkworm moth's life, viz., mating and egg-laying.

Males mate with headless females, and the headless females, after mating, lay a few eggs which develop normally, that is become fertilized by the release of spermatozoa from the spermatheca in the female's body, are oviposited by the repeated extrusion and retraction of the ovipositor, and make the usual color changes (from yellow to cherry-red and then to lead-gray) incidental to normal development. But in no case did a headless female lay her full complement of eggs, in fact in no case were more than a score of eggs laid (the normal number is from 200 to 350). Headless females (and headless males) usually live as long as unmutilated individuals, *i. e.*, from a week to two weeks.

Females with head and thorax cut off (and even part of the abdomen) can be mated with by males, and this fractional part of the female can fertilize and oviposit a few eggs which begin normal development. In one case 10 eggs, of which 8 are now normally developing were oviposited by such an impregnated part of female abdomen, this abdominal relict remaining alive (!), *i. e.*, flexible and responsive to stimulus and capable of extruding the ovipositor and laying eggs, for forty hours.

Males with head removed cannot find females, nor can they mate if placed in contact with them. When the head or head and prothorax of a male is cut off immediately after the male and female are *in copulo* the female, although uninjured, lays no eggs. If heads of both males and females *in copulo* are removed no eggs are laid although both moths remain alive usually as long as do unmutilated individuals.

A silkworm moth can maintain itself right side up with antennæ off or with antennæ off and eyes blackened, but with head off one position seems indistinguishable from another to it, *i. e.*, it lies on one side or the other, on the venter or dorsum equally willingly. The organs of equilibrium are not on the antennæ, then, but are lost when the rest of the head is removed.

STANFORD UNIVERSITY, CALIF.,
October 15, 1906.

AN ABNORMAL CESTODE PROGLOTTID.[1]

EDWIN LINTON.

In the summer of 1905, while engaged in work for the Bureau of Fisheries at the Woods Hole Laboratory I found an interesting cestode abnormality, a description of which is here given.

Among a lot of free segments of the cestode *Calyptrobothrium occidentale* Linton from the torpedo, I noticed one which had two reproductive apertures upon one of the lateral margins. Upon flattening this segment under a cover-glass it was found to be double. The reduplication can be best explained in general by saying that it is such as would be formed if two normal proglottids were to grow together by their anterior ends.

The specimen was fixed over a flame, and after the customary hardening was stained with borax carmine and mounted in balsam. Fig. 1 was sketched from the mounted specimen. The specimen measured 4 millimeters in length and 2 millimeters in breadth.

As may be seen by an examination of the figure the specimen would give rise to two complete proglottids if it were transversely bisected midway between the two reproductive apertures. At the opposite ends will be seen the lobed ovaries (*o*, *o*) arranged symmetrically on either side of the median line, with the shell gland (*sg*, *sg*) between the two lateral masses of the ovaries and toward the extremity of the proglottid.

The reproductive apertures are on the same lateral margin, each being approximately not far from one third the total length of the double segment from one end.

Each of the two parts, considered by itself is a normal segment, so far as the general arrangement of the various organs is concerned, except that there is relatively less space taken up by the testes (*t*) which are massed together in the median region and possessed in common by the two component parts of the double segment.

The vitelline glands (*vg*, *vg*) are continuous along the margin

[1] Published by permission of the Bureau of Fisheries.

opposite the reproductive apertures. On the opposite margin a vitelline mass separates the two vaginæ and, like the testes, belongs to both components of the double segment.

There is no line of demarcation between the two components. The margins are continuous and smooth everywhere except between the reproductive apertures where the minute serrations, which are characteristic features of younger portions of the strobile, are seen. These serrations are inclined towards the extremity of the smaller part, and may be taken as belonging to that part.

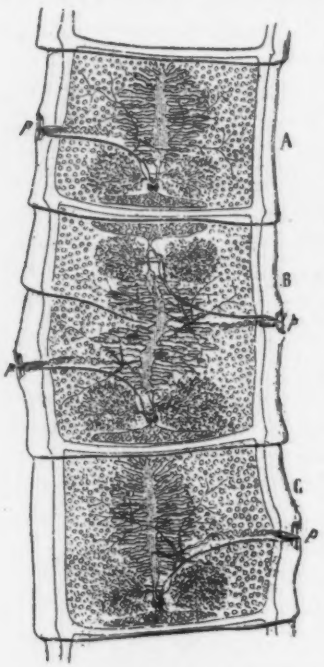

FIG. 2. After Blanchard. Abnormality of genital organs of *Tænia saginata*. *A*, *C*, normal segment; *B*, abnormal segment.

There is no indication as to which is the older of the two parts, except a slight difference in size. Evidently the reversal took place very soon after the primary segment was formed. Although the segment was not seen attached to its strobile it is not conceivable that the abnormal condition was assumed after separation from the strobile.

It is to be noted that there is a reversal in a dorso-ventral direction also, the vagina and oviduct lying above the uterus in one part and below the uterus in the other. Or, to state this comparison in another way, if the specimen were folded together on a hinge-line crossing transversely between the vaginæ the two components would not be symmetrical to the plane of their apposed faces, but one would correspond in the position and arrangement of the parts to the other.

Abnormalities in cestodes are of common occurrence and the

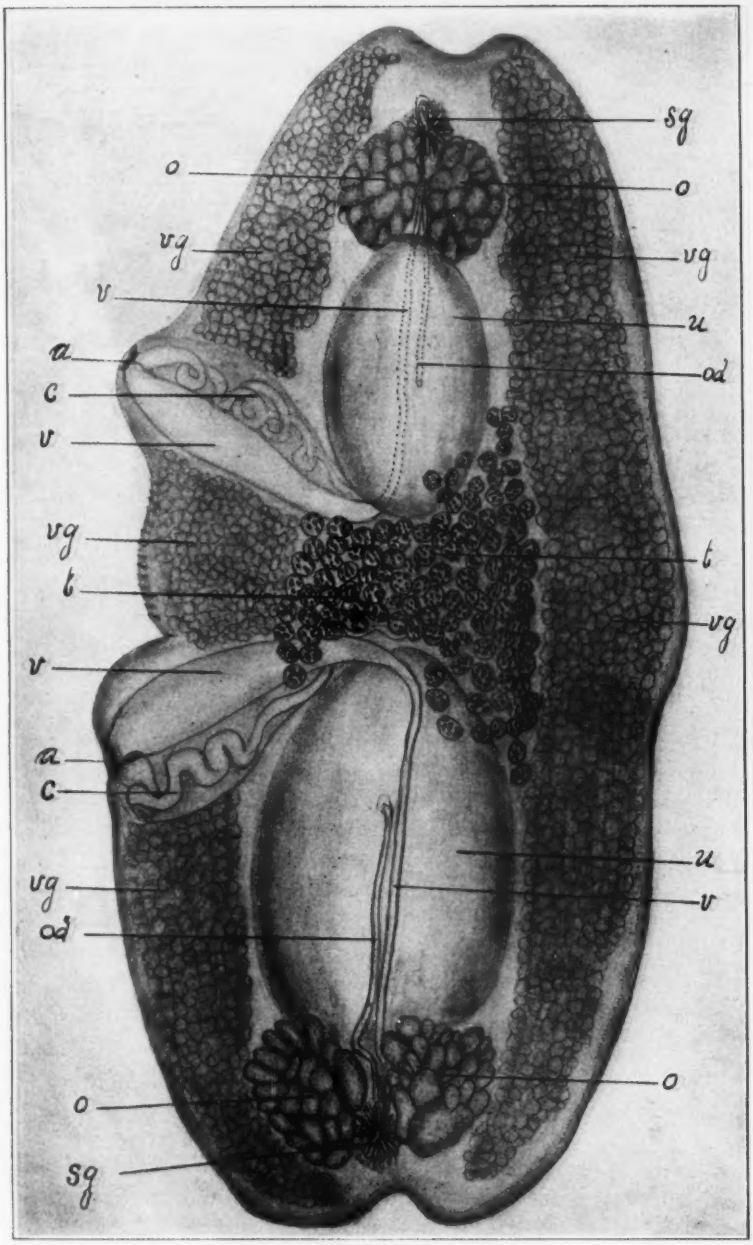

FIG. 1. Abnormal segment of *Calyptrobothrium occidentale* Linton from the torpedo. Actual length 4 millimeters, *a*, reproductive aperture; *sg*, shell gland; *c*, cirrus; *t*, testes; *o*, ovary; *u*, uterus; *od*, oviduct; *v*, vagina; *vg*, vitelline gland.

literature of the subject is considerable. The only case, however, which at all resembles the subject of this sketch, that I find in the literature of the subject, to which I have access, is the one recorded by Blanchard for *Tænia saginata* (*Bulletin de la Societé Zoologique de France*, 1890, XV., 166–168, and reprinted in *Progrès Médical*, July, 1894).

My friend Dr. Stiles informs me that, while he has repeatedly found abnormalities in cestode segments, he has not made any record of any cases such as is described in this paper.

On account of the unique character of this abnormality, therefore, and for purposes of comparison I reproduce Blanchard's figure (Fig. 2).

In Blanchard's specimen the ovaries and vitelline glands are at opposite ends of the abnormal segment; the testes are continuous along the lateral margins; the reproductive apertures are on opposite lateral margins; the uterus is common to both parts. At about one third of the length from the anterior end there is a transverse incision which reaches to the median line, and is followed on its side by a perfectly normal segment. If this incision were to extend somewhat diagonally across, so as to reach the other margin behind the reproductive aperture, there would then be a single inverted segment intercalated between two normal segments.

It should be stated here that the abundance of material found in the summer of 1905 furnishes additional data, which will make it necessary to separate the two varieties noted in the original description (see Bulletin of the United States Fish Commission for 1899, p. 298) into two distinct species.

The abnormal segment belongs to the larger variety which will retain the name *C. occidentale*.

WASHINGTON AND JEFFERSON COLLEGE,
December 1, 1906.

OBSERVATIONS ON THE YOUNG OF RANATRA QUADRIDENTATA STAL.

S. J. HOLMES.

In two previously published papers [1] I have described certain features of the behavior of the water scorpion, *Ranatra*, and as opportunity presented itself this last spring of obtaining young *Ranatras* in abundance attention was devoted to a comparison of the behavior of the young and the mature forms. The various stages in the metamorphosis of the nymph were followed, but as these have recently been described by Torre-Bueno [2] the observations made on this subject are omitted.

Ranatra lays its eggs in the spring commonly in the stems of aquatic plants or floating pieces of wood. The eggs are inserted in the material containing them so that they are nearly buried. They are of cylindrical form, rounded at either end, and provided at the outer end with a pair of slender filaments of uncertain function. When one sees a *Ranatra* which has recently emerged from the egg he cannot but be surprised that the young insect should have been enclosed in so small a receptacle. The body of the young *Ranatra* is as broad as the egg and over twice as long. The length of the young, measured from the end of the proboscis to the tip of the breathing tube is frequently 8 mm., while the egg itself is only about 3 mm.

The young in general appearance closely resemble the adult form. The prothorax, however, is relatively shorter, the wings are entirely absent, and the breathing tube, or what functions as such,[3] is relatively short, being about one fourth of the length of the body, while in the adult it is about four fifths the length of the body. At first the young are very soft. The slender legs bend with the greatest ease, and if the insect is taken out of the

[1] Holmes, "The Reactions of Ranatra to Light," *Jour. Comparative Neurology and Psychology*, Vol. 15, p. 305. "Death Feigning in Ranatra," *l. c.*, Vol. 16, p. 200.

[2] Torre-Bueno, *Canadian Entomologist*, Vol. 38, p. 242, 1906.

[3] Torre-Bueno, *l. c.*, has shown that the so-called breathing tube of the young nymph differs essentially in structure from that of the adult insect.

water it is unable to support itself and wriggles about helplessly. Its integument rapidly hardens, however, and in the course of a few hours it is able to move around out of water as well as an older individual.

When first hatched the young are pale in color, but they soon become much darker, many specimens becoming quite dark in less than a day.

The manner of walking, swimming, turning over when placed on the back, and the attitudes assumed when resting at the surface of the water, or in contact with objects below the surface, are very nearly the same as in the mature insect. Soon after hatching the young *Ranatras* take up a position at the surface of the water with the tip of the breathing tube just projecting through the surface film and the body inclined obliquely downward. The second and third pairs of legs are held in a sprawled out position, while the first pair is held in front, and bent upward at the middle, with the claw held open. The position is one of readiness for quickly seizing any small object that passes within reach. Young *Ranatras* are remarkably active in the capture of prey. Any small object that strikes the outstretched arms is grabbed at with surprising quickness. If a small insect or crustacean is seized, it is drawn towards the mouth, usually with the assistance of the other arm, and the proboscis is moved about over it in the endeavor to find a soft spot through which it can penetrate. When this is found the juices of the body are gradually sucked out and the rest of the prey rejected. Young *Ranatras* will seize and suck out almost any animal not of too large size. I observed one not a day old deftly catch a small ostracod that happened to swim against one of its outstretched arms. The ostracod tightly closed the valves of its shell, but the *Ranatra* turned it over and over, exploring all sides of it with the tip of its proboscis and endeavoring in vain to force an entrance between the valves. After the round smooth ostracod was rolled about for several minutes it slipped from the grasp of its captor and swam away.

Ranatras may readily be fed by seizing a small organism in a pair of pincers and carefully bringing it up to them. Animals as large as themselves are successfully coped with. Large *Hyalel-*

las are seized and sucked out without much difficulty. While mature *Ranatras* will live together peaceably for a long time the young readily attack and devour one another. If several young are kept in the same dish it will be found that, in the course of a few days, a majority of them will have fallen victims to a few successful combatants. If a young *Ranatra* seizes another near the middle of the body it is usually able to bring its victim up to its proboscis, the tip of which is moved about in search of a soft spot in the armor of the unfortunate individual, whose blood is then deliberately sucked out notwithstanding the creature's struggles. Often a *Ranatra* is seized by one of its legs. This is usually not resented until its captor, after pushing the tip of its proboscis along the leg until it finds one of the joints, begins to insert its piercing stylets through the soft integument, when a vigorous struggle ensues.

Young *Ranatras* are exceedingly voracious creatures, as they will kill and suck out several insects as large as themselves in the course of a day. Their food consists mainly of small swimming forms, chiefly small crustaceans and insects, which come near the surface of the water. Like the adults, they are very efficient enemies of the larvæ of mosquitoes. They do not pursue their prey, and they seldom catch forms that keep in close contact with solid objects. They are like so many traps set ready to seize anything that comes in contact with them. Often, however, an object is grabbed at if it passes near a *Ranatra* without coming into actual contact with it. This action is probably a response to the impact of the water. If a *Ranatra* is hungry, touching the surface film with a needle near the insect will often cause it to grab about wildly in the effort to seize whatever may have caused the disturbance. An object of too large or threatening appearance causes the young *Ranatra* to jerk back its first pair of legs, but there are no efforts to swim away from danger. When this reaction occurs the insect cannot be induced to take food for some time.

The reactions of young *Ranatras* to light are not nearly so vigorous and decided as those of the adult. A feeble positive phototaxis is manifested the first day after hatching and increases gradually as the insect grows older. Individuals a week old are

very often found swimming on the side of the dish towards the light; if the dish is turned about they quickly swim back again to the light side. When out of water they are comparatively irresponsive to light — a fact in marked contrast to the behavior of the mature insects. Movements of the head in response to changes in the position of the light, which are so pronounced in the adults are manifested in the young of a week old or even less, but they are not very pronounced. When out of water the young could not be induced to walk toward the light or respond to it in any other way than by making rather feeble movements of the head. While contact stimuli applied to the mature insects when in the water cause a negative phototaxis, they failed in the forms experimented with to produce this effect in the young.

The death feigning of young *Ranatras* is not so decided or prolonged as in older specimens, and it also differs in certain other particulars. Young *Ranatras* when taken out of the water and laid on a table frequently become immobile in whatever position they may happen to lie. Neither in the young nor the mature form do the appendages assume any definite position such as they do in the death feint of many other insects. The feint is shown during the first day of free life. The muscular system gives evidence of a certain degree of rigidity, but owing to the flexibility of the appendages this is not so clearly manifested as in somewhat older individuals.

In specimens five days old the death feint is more decided. Several specimens of this age were taken out of a dish and laid on a table. Immediately they all became immobile. They could be picked up by one of the slender legs and held out without causing a bend in any of the joints, thus showing that the muscles were in a state of extreme contraction. Many specimens would endure considerable handling and poking about without making any response. In some cases such treatment would bring them quickly out of the feint, and all the forms experimented with were brought out of it by more prolonged stimulation. In this respect the young differ from the mature insects which will endure a great deal of maltreatment without making any response.

In specimens coming out of the death feint handling or rubbing them with a dry camel's hair brush produced in some cases a

resumption of the feint; in others it had no effect. This, too, is different from the characteristic reaction of the adults which, when they awaken from the feint, can readily be caused to resume feigning many times in succession by handling or gently stroking them. And if an adult is picked up while feigning it is rarely brought out of its feint by this means.

It is a curious fact that while the mature *Ranatra* will endure all sorts of maltreatment during the death feint, even suffering its legs to be cut off one by one or its body cut in two without the least response, the moment the insect is placed in the water the death feint entirely disappears. There is no way in which the feint can be terminated so quickly and completely as by this means. Nor is it possible by any sort of manipulation to cause the insect to feign death so long as it is in the water. It is certainly remarkable that an insect that will feign, it may be for hours, with its muscular system tense so that all its appendages are perfectly stiff should so completely and suddenly change its behavior when it is placed in another medium.

In *Ranatras* of five days old or less the death feint often persists for a time after they are placed in water. They do not, as a rule, swim directly away, as the adults do, but frequently remain motionless and apparently still for several seconds, or in some cases for over a minute. When in the air the duration of the death feint of the young is increased if they are kept wet. Specimens that refuse to feign when rubbed with a dry camel's hair brush can commonly be made to do so by rubbing them with a brush dipped in water. And when specimens cannot be induced to feign by this means they can generally be thrown into a feint by dipping them into water and then leaving them on the table. Dryness produces in the young a restlessness that is not shown by the adult, — a result not improbably due to their less ability to withstand lack of water.

The young, like the mature forms, can be cut in two while in the death feint without causing any response. A specimen which was cut across near the middle of the body showed no movement in either piece; the legs were rigid, but after being poked about for some time they began to move. Handling the anterior piece failed to cause it to feign again, but when it was dipped into the

water and placed back on the table it feigned for several minutes, the legs giving the same signs of muscular rigidity as before. Several times it came out of its feint and as many times it was caused to resume feigning by dipping it into water and placing it on the table. Contact with a wet camel's hair brush would readily cause it to feign, but a dry brush would produce no feint, or but a very short one. Other experiments gave very similar results.

It is difficult to understand how the death feint in *Ranatra* can be of much value to it. While the European *Ranatra linearis* has been known to fly to lights at night (a rare occurrence apparently) I have been unable to obtain any evidence of such a habit in any of our American species. In fact *Ranatra* very seldom leaves the water of its own accord on account of any sort of inducement, and one is therefore strongly inclined to believe that the death feint which is manifested only when the insect is in the air is rather an incidental result of certain physiological peculiarities of the organism than an instinct which has been built up by natural selection for the benefit of the species. We must adopt such a view, I think, regarding hypnotism in the higher animals and in man; for what selective value can it be to a species, such as our own for instance, to possess the capacity of being thrown into the hypnotic state? The instinct of feigning death is of unquestionable service to many forms, and it is possible that in rare instances it may have proven of selective value to *Ranatra*, but it is open to serious question if the instinct in this form has been evolved because of its importance as a means of protection.

The strong and at times almost violent positive phototaxis which *Ranatra* exhibits presents another problem of the same kind. Certain of the most striking features of this reaction are manifested only when the insect is out of water. As a rule *Ranatra* inhabits more or less shaded retreats among submerged grass or weeds near the water's edge. It is kept in such situations, partly through the direct effect of its positive thigmotaxis, and partly because contact stimuli (as shown in a previous paper) cause it to become negatively phototactic. The positive phototaxis which appears when the insect is swimming freely in the

water is certainly of no service to it in leading it into its accustomed habitat if it should, for any reason, become removed from it. In the air and near a bright light *Ranatra* becomes, sooner or later, strongly positive, often being wrought up to the highest pitch of excitement in its efforts to reach the light. Of the utility of such curious behavior it is indeed difficult to conceive a reasonable explanation.

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A STUDY OF FUNDAMENTAL BARS IN FEATHERS.

OSCAR RIDDLE.

The structure and development of feathers have been studied by many investigators. The pigments of feathers have also been the subject of a very great number of researches. In spite, however, of these numerous studies of feather structures and pigments, we know almost nothing of structural differences between pigmented and non-pigmented areas, and nothing at all of the causes which lead to the orderly and definite distribution of pigment into the often complex color-patterns commonly found in birds. In connection with a research directed to these two points it was thought advisable to make a study of certain *defects* which were known to appear occasionally in feathers. It is a preliminary account of my results in this more restricted field — which, however, proved to be a rather significant one — that is to be found in this paper. The work was undertaken in 1904 under the direction of Professor C. O. Whitman in the zoölogical laboratory of the University of Chicago. It is a pleasure to acknowledge the help, encouragement and criticism which Professor Whitman has given in connection with this work.

At the time I took up the study of the defects under consideration, they had been reported but once, and this report had to do with but a single specimen, a single plumage, and a single defect in each feather. This was an account by R. M. Strong[1] of "A Case of Abnormal Plumage" found in a hybrid pigeon. Dr. Strong described and figured two types of abnormalities, and concurred with Professor Whitman, who had reared the bird, in the opinion that the defects were probably caused by malnutrition during the growth of the juvenal plumage. Besides this case, Professor Whitman had observed these or similar defects in the feathers of several of his birds, and my problem was to learn the extent of their occurrence and to determine their cause. In the course of my studies I have found still other abnormalities —

[1] BIOLOGICAL BULLETIN, November, 1902.

or rather, different forms of the same defect — and I shall first give a description of the nature of the defects, and later consider the question of their extent and cause.

Defects in Adult Morphology. — In the adult expanded feather, I have found five types of defects in structure. In Fig. 1, *a* is shown the first type. There is in this case a sharply defined area extending entirely across the feather-vane, in which there are no, or very few, perfect barbules. A cross-section of the feather at this point would show only shaft and barbs. One such area in the entire length of the feather was one of the types described by Strong. I find, however, an abundance of cases where such areas occur at regular intervals practically throughout the length of the feather. This regularity in the spaces separating the defects, indeed, furnished the clue to the nature of the latter. It will be seen that these areas cross the barbs in such a way as to form almost a right angle with them. The same thing is true of the other types of defects and argues for their standing primarily all for the same thing.

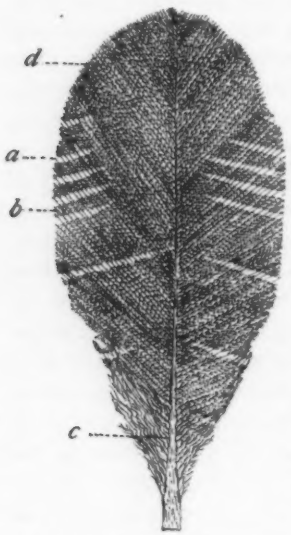

FIG. 1. Feather from a poorly nourished chick showing abnormalities. *a*, abnormal area; *b*, 'fundamental bar' (a day's growth); *c*, constrictions; *d*, region in which defective lines showed plainly in this feather. (× 2.)

The second type represents the greatest extreme to be met with among these abnormalities. The feather in the abnormal region has been reduced to shaft only; both barbules and barbs are gone. The second of the defects described by Strong evidently belonged to this type, though he states that there was no shaft present in his material and that its place was taken by a small cylinder of fused barbs. I have not seen just such a structure as he describes; but it is rare and doubtless is to be regarded as a sort of record of the very severest conditions which

a bird can encounter and endure. In types one and two the barbs and shaft are often bent or kinked in the abnormal region.

The third type of defect is something very much less conspicuous than either of the two types already considered. It could not be represented in the drawing. It is a very minute depression extending across the upper and dorsal surface of the feather. It is not always easy, however, to determine that it is a depression at all. It often seems a line, or simply the point of union of a distal with a proximal part of the feather-vane. This line crosses a series of barbs making with them a right angle as did the defective area of type one. These lines or depressions are usually so inconspicuous that even close observation may not reveal them. Yet they exist and can be demonstrated in all feathers, and at any level throughout the length of the feather.

The existence of these depressions as normal occurrences in the feather is apparently nowhere mentioned in the literature. Certainly their significance has not been made known. As may be inferred from my classification of them, I have found them to bear a close relation to the defective feather areas. These lines which are thoroughly characteristic of feathers are properly classified among feather defects, for, it is always at these lines that the defects like those of types one and four appear and, moreover, they show all possible gradations into types one and four. I shall hereafter speak of defects of this type as *defective lines*, or depressions; those of type one as *defective areas;* those of type four as *constrictions.*

FIG. 2. Entire feather-germ from *Cardinalis virginianus* showing constrictions. (Actual length 13 mm.)

It is those feather-vanes which are made up of a series of deep depressions or constrictions that show the defects of type four. I shall say nothing here of the conditions represented in this type, but perhaps an idea can be had from the feather germ shown in Fig. 2.

Of type five, I have seen but a single example. In this the defect extends vertically or the long way of the feather. The barbs of one half of the vane have their distal portions broken

away at even distances from the shaft. Duerden[1] states that this abnormality is also very rarely met with among ostriches.

The recognition of the defective lines in all feathers throws a new light on abrasion and wear in feathers. That there are birds which "normally" have the barbules broken off at certain fairly definite points in the more distal barbs has been observed by Meves,[2] Chapman,[3] Dwight,[4] Strong[5] and others. Meves and Chapman have noted, too, that the barb itself may be broken near the distal end. I have seen several cases of the breaking of a series of barbs at the point where they were crossed by the same defective line, and I believe that further study will prove that most feather abrasions occur by the space between two defective lines breaking away as a single piece.

The Defects in Feather-germs. — I have been able to observe the defects in several formative stages. I shall say only a word concerning them here. The prominent defects in the unexpanded germ are easily recognized by the unaided eye; sometimes they appear as definite constrictions (*Cardinalis virginianus*, see Fig. 2, *a*.), but very often as points of a different color (rectrices of *Turtur risorius*). A microscopic examination of a region which would develop a defective area shows a reduction of cell-growth and division particularly in the region of the barbules.

Extent and Distribution on the Abnormalities.

In the Bird Groups. — In looking for the cause of the defects one turned naturally to the birds to find whether they were widespread or restricted phenomena. I stated that at the time the present work was begun, there was in the literature but a single account of them, and that account had to do with a single specimen —a hybrid pigeon. Recently Professor J. E. Duerden has

[1] Duerden, "Bars in Ostrich Feathers," *Agr. Jour. Cape of Good Hope*, May 1906.

[2] Meves, W., "Über die Farbenveranderung der Vogel," *Jour. für Ornith.*, Bd. 3, 1855.

[3] Chapman, F. M., "On the Changes of Plumage in the Snowflake," *Amer. Mus. Nat. Hist.*, vol. 8.

[4] Dwight, J., Jr., "The Sequence of Plumages and Moults in the Passerine Birds of New York," *Ann. N. Y. Acad. Sci.*, vol. 13, No. 1.

[5] Strong, R. M., "The Development of Color in the Definitive Feather," *Bull. Mus. Comp. Zool.*, vol. 40, no. 3.

reported the abnormality in the ostriches, particularly in those of South Africa. I learn from him by letter that he has undertaken a thoroughgoing research to determine the cause of the "barring" so prevalent in the ostriches. He estimates that the value of the ostrich plumes from South Africa alone are from this cause depreciated in value to the extent of £250,000 annually.

The defects are, however, not confined to hybrid pigeons and domesticated ostriches. I find them in the most widely separated bird groups; in primitive and in recent birds; in land and in water birds; in domesticated and in wild birds; in birds from the arctic and from the torrid zone, etc. I have been able, owing to the courtesies extended by Professor C. B. Cory and Dr. Ned Dearborn, of the Field Columbian Museum in Chicago, to examine a very great variety of birds belonging to the Museum. I find that although it is not easy to see evident defects in every specimen, it is easy to find them in every species. We may conclude therefore, that they are to be found in *all* birds.

It is a fact, and a significant one I think, that the defects are, in general, more common in domesticated and caged birds than in wild birds. In this connection, however, it should be stated that the defects appear indifferently in pure breeds, hybrids and mongrels. At any rate I have verified this in a number of our domesticated birds.

On Individual Birds. — I have found the defects in all of the plumages of the birds, with the possible exception of the first or downy plumage. In some birds the defects seem to occur more frequently in the juvenal (of Dwight) than in the others. The emphasized defects appear in all the feather-tracts or pterylæ; but in a particular bird, and usually in a particular species, certain tracts show them in greater numbers than do others.

In an Individual Feather. — In the feather there may be produced at any point in its length, either of the five types of abnormality. In some birds (*Gallus*) the distal part of the feather oftener shows the defective *areas;* the proximal end, the deep *constrictions*, while we get defective *lines* in one form or another at every point in the feather's length.

The Meaning and Cause of the Defective Lines and of the Spaces Between Them.

We may now consider the significance of this blocking out of the feather from end to end into bands, "bars," or plane feather-elements, separated from each other by extremely faint depressions or constrictions — for, my studies demonstrate that this is a true conception of feather structure.

That the feather from tip to tip does not represent a perfect, uniform continuity, but is made up of an apposed series of faint "fundamental bars" is a conception which I owe to Professor Whitman. I have proved absolutely that the defective lines, or points of apposition of the "fundamental bars" are the points at which all of the defects appear, and are therefore, really miniature representatives of the defective areas and constrictions of types one and four. I think I have also proved that each block, segment or "fundamental bar" of the feather represents a day of growth, and this is at the same time the amount of feather-growth between two low blood-pressures. Further, I have abundant evidence that the defective lines and areas represent points developed under a diminished rate of cell-growth and cell-division, brought about by a reduced nutrition, which is in turn the result of a daily lowering of the blood-pressure. This low blood-pressure doubtless occurs between one o'clock A. M. and six A. M.

The evidence that a single "fundamental bar" and a single defective line or area are laid down each day, and that this is the total of a day's growth is conclusive. In very favorable material I have been able to show, for example, that a feather 56 days old shows 56 "fundamental bars" and 56 defective lines, areas and constrictions. That the defective area is laid down at night and during a period of low blood-pressure, I have demonstrated twice experimentally. A chick was kept on two succeeding nights, from 8 o'clock P. M. till 8 A. M. in an atmosphere containing amyl nitrite (which lowers the blood-pressure).[1] This bird later showed two emphasized defective areas in the region of the feather produced during the two days of the experiment, and these areas occupied the region normal to the defective lines and

[1] The effect of several drugs on the blood-pressure of birds has been investigated by Dr. S. A. Matthews and the writer. Our results are soon to be published.

did not appear in the territory occupied by a "fundamental bar." Since these defective lines are laid down at approximately the same time each day — as is proved by the regularity in the distances separating them — we are forced to the conclusion that the defective *lines* are normally laid down at night, and that a lowering of the blood-pressure is associated with the production of defective *areas*, and, therefore of defective lines, for, that the defective line stands for the initial stage of the defective area is as certain as that an area has more dimensions than a line. The evidence in part is, that one sees all possible intergradations, that each marks off a day's growth, that when the area occurs it always falls in the place for the line, that a certain part of the line only may be transformed into the obviously defective area, etc. That there is a reduction of cell-growth and cell-division in the defective area is proved absolutely by an examination of the adult morphology of an exaggerated defect, as it is also by the histology of the defects in the feather-germ.

That the low blood-pressure occurs at night is evidenced by the experiment of the chick in the amyl nitrite. That it occurs between midnight and six in the morning may be inferred from the fact that the lowest daily *temperature* in birds falls between these hours. Reasoning from the facts known in mammals we may assume that the minimum blood-pressure coincides in point of time with the minimum temperature. I have not been able to get the daily blood-pressure curve of birds, owing to the difficulty of doing so in birds of small size. The ostriches might well be used for that purpose. At this point I may suggest that the ostriches will doubtless cease to interpolate defective *areas* in their plumes as soon as they can find the perfect diet, and the various life conditions which will give them *well-nourished bodies* and strong, *effective circulations*. After all, these two are one.

The Relation of Nutrition to the Defects.

At the very beginning of this study, it was thought that the defective areas stood in a certain relation to a faulty nutrition. A number of experiments were made to determine this. A number of young ring doves were alternately starved and fed, with the result that in these birds the defective areas appeared in the

juvenal plumage in great numbers. The same experiment was tried on young chicks with the same result. It was noticed, however, that notwithstanding the careful and plentiful feeding of the control, an occasional defect could be found in their feathers too. These experiments[1] showed that malnutrition is beyond doubt the important factor in the production of the defective areas, but apparently not the only one. An experiment was then carried through to learn whether the defects found in the control could be produced by the usual *handling* of the birds, and perhaps slightly crumpling their feather-germs. The results were negative; but it was found that when the feather-germs were *strongly crumpled* and broken in the region of feather growth, the defects were readily produced.

During the progress of an experiment on some young chicks (carried on for a quite different purpose) it was found that chicks which were fed on the fat stain Sudan III produced the defective areas in much greater numbers than did the control birds. It was determined that the ordinary variations of light, temperature, etc., did not cause the defects. The net result so far of all the experiments for the determination of the cause of the defects, indicated that those things which interfere with the *nutrition* of the feather-germ will produce the defects, while those things not capable of affecting the nutrition will not produce them. It is easy to understand how a crumpling of the feather-germ would temporarily interfere with the circulation within it. In the chicks fed with Sudan III. it was evident that a sort of "starving" effect was produced by it. By the time the experiments had proceeded thus far I knew that a day of normal growth in a feather is represented by a "fundamental bar" and a defective line, and also that a defective line stands in close relation to a defective area. This suggested that the defective areas in the control, and the defective lines in all feathers, are produced by an internal factor with a definite rhythm, and that the rhythm is able, like my experiments, to effect the nutrition of the feather elements. This recommended blood-pressure to me, and the experiments were made with the result stated above.

Blood-Pressure and Temperature Rhythms. — I shall not here

[1] Partial results of these feeding experiments were communicated by letter to Professor Duerden and were published in his paper, cited elsewhere.

attempt to explain the causes for the nightly fall of the blood-pressure in birds. Let it suffice to say that we find a parallel phenomenon in mammals. I wish further to call attention to the fact that my demonstration that the lowest blood-pressure in birds falls at night is evidence that the blood-pressure and temperature curves of birds are similar curves, as they are known to be in mammals. Of course, I have not showed a blood-pressure *curve* for birds; I have, however, located in a general way the *time* of its *minimum*. I am in a position to confirm the observations of Corin and Van Beneden[1] as to the temperature curves of birds. They worked with pigeons. I have temperature curves essentially similar to theirs, from ducks, ring-doves, and from chicks both old and young. The lowest temperature occurs at about four to five o'clock A. M.

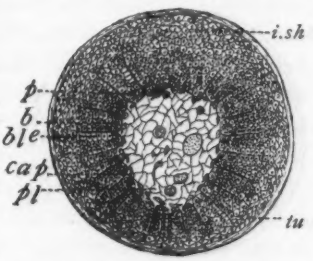

FIG. 3. Cross-section of a feather-germ in the region of growth. (Semi-diagrammatic, magnified about 100 diameters.) *b*, barb-forming cells; *ble*, barbule-forming cells; *p*, pigment cell; *cap*, capillaries; *pl*, pulp; *tu*, outer sheath; *i.sh*, inner sheath.

Low Blood-Pressure and the Nutrition of the Feather Elements.— There remains to be indicated some of the histological relations of the capillaries and the feather-elements which suffer from the lowering of the vascular tension. I shall also outline the way in which the low pressure probably acts.

Just as among the vertebrates we know that certain tissues, *e. g.*, the liver cells, are kept always on the verge of asphyxiation, so I believe are the epidermal cells of the growing feather-germ taxed to their utmost to secure from the blood enough nourishment to allow the rapid cell-division to proceed in full swing. Where else in an adult vertebrate do we find a more rapid growth and differentiation of tissue than we find in the moulting of certain birds? We may then expect to find here a struggle for food when this becomes reduced in amount, and those parts nearer the blood-supply should fare better than parts

[1] Corin, G., and Van Beneden, A., "La Régulation de la tempérarure chez les Pigeons," *Archives de Biologie*, Vol. VII., pp. 265–276, 1887.

more removed. Now this is exactly what happens. The capillaries (Fig. 3 *cap*) of the feather-germ lie nearest those cells which enter into the formation of the *barbs* (Fig. 3, *b*) and these are able to continue to grow even with a weakened food-supply; they too, though, are suppressed in cases of extreme starvation. The cells which form the *barbules* (Fig. 3, *b*) are not in contact with capillary walls, and can utilize only the surplus of food which filters through the barb-forming cells. With this fact in mind it is clear that we should expect a diminished food-supply to first check the growth in the barbules and that still further reduction is necessary to check the growth of the barbs. Experience proves that this is true (I use the words "food" and "nutriment" in a broad sense, and *oxygen* is to be read into them). It is conceivable that a reduced oxygen-supply is here playing a part, since in all my experiments and in any normal lowering of the blood-pressure, the available oxygen is decreased.

From what has just been said of the filtration method by which the barbule cells receive their nutriment, we can now see how it is that blood-pressure plays so important a part in the production of defective areas. It is well known that when a period of low blood-pressure sets in, the lymph begins to flow from the spaces between the cells of the body into the capillaries. Thus, by withdrawing a quantity of food from the immediate environs of the cell, a low blood-pressure affects the cell in the same way as does an actual reduction of the amount of nourishment circulating in the blood.

It appears, therefore, that the feather germ as it grows and unfolds, spreads before us a record of some earlier significant occurrences within. Indeed, it now seems certain that the delicate filaments, so admirably interlaced to form a feather-vane, are as capable as a revolving drum of recording the important changes in vascular pressure. To be sure, the tracings on the plumes are not to be measured as symmetrical curves with a definite number of millimeters of daily variation, but are written in "fundamental bars" separated by areas more or less imperfect which are to be read in terms of cell-growth and cell-division.

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December, 1906.

STUDIES ON THE RELATION BETWEEN AMITOSIS AND MITOSIS.

II. Development of the Testes and Spermatogenesis in Moniezia.

C. M. CHILD.

The material for this study was obtained from the same species, *viz.*, *Moniezia expansa* and *Moniezia planissima*, as that of the first paper of this series[1] and most of it, in fact from the same chains. The methods of fixation, observation and record are the same as those already described in that paper. Various details in the spermatogenesis are only briefly considered, since they are not directly connected with the chief purpose of the paper.

I. *The Formation of the Testes.*

The testes develop from cells of the parenchyma which do not differ visibly from other cells of the same region. They appear in the dorsal region of the central parenchyma. Before their appearance two kinds of cells are visible in the parenchyma: one of these is smaller and surrounded by more or less cytoplasm apparently without definite boundary and usually elongated in the dorso-ventral direction, with one or more fibrillar extensions at each end. Figs. 1, *A–D* (Pl. VII.), show parenchymal cells of this kind in the earliest stages of testis formation. Amitotic division of the nucleus is occurring in each case. Fig. 1, *A*, shows a case in which the two parts of the dividing nucleus stain differently Fig. 1, *C*, a case of the endogenous form of nuclear division which was described in the preceding paper, while Figs. 1, *B*, and 1, *D*, show late stages in division, the one by constriction, the other by formation of a nuclear plate. For a description of these and other forms and stages of amitosis in *Moniezia* the reader is referred to the preceding paper of this series.

The other form of cell existing in the parenchyma before testis

[1] Child, "Studies on the Relation between Amitosis and Mitosis I. Development of the Ovary and Oögenesis in Moniezia," Biol. Bull., Vol. XII., No. 2, 1907.

formation is much larger, and its cytoplasm is highly vacuolated and more distinctly bounded from the parenchymal matrix about it. These cells appear always to be connected with deeply staining fibers which extend dorso-ventrally across the central region of the proglottid and which I take to be dorso-ventral muscle fibers since they and the cells connected with them are similar to those of the muscular layers. Fig. 2, *A* (Pl. VII.), shows one of these cells with a portion of its fiber. The fiber passes directly through the cell-body on one side of the nucleus and the cytoplasm extends visibly for a considerable distance along the fiber. The evidence that these cells develop into testes is very strong. Fig. 2, *B* (Pl. VII.), represents a section through nucleus and body of one of these cells in which the nucleus is apparently undergoing amitosis. Whether this particular case would have developed into a testis it is of course impossible to determine. But Figs. 2, *C*, and 2, *D* (Pl. VII.), represent characteristic cases slightly more advanced. Here several nuclei are contained in a space which corresponds closely with the form of the muscle cell and contains what seem to be strands of the old vacuolated cytoplasm, while about some of the nuclei a layer of more deeply staining cytoplasm is visible, apparently in process of formation. Through the space which apparently represents the region previously occupied by the body of the muscle cell passes the fiber. The presence of the fiber and the well marked outline of the space seem to me to constitute very strong evidence in favor of the conclusion that each of these groups of nuclei have arisen by the division of a nucleus of a muscle cell. That these groups develop into testes there can be no doubt. Their development can be followed from proglottid to proglottid without the slightest difficulty, and there are no other similar groups of nuclei in the parenchyma. Fig. 2, *E* (Pl. VII.), shows a case in which the muscle fiber is apparently undergoing degeneration. In all of these cases amitotic division of the nuclei is taking place. The figures give only a few examples of the cases observed. In a brief account of the history of these cells already published additional figures are given.[1] If these observations are correct, and I have, so far as

[1] Child, "The Development of Germ Cells from Differentiated Somatic Cells in Moniezia." *Anat. Anz.*, Bd. XXIX., Nos. 21 and 22, 1906.

I am aware, taken all possible precautions to assure myself that they are, it seems impossible to escape the conclusion that in *Moniezia* the male germ-cells may develop from cells which have previously been differentiated and functional in the soma. Generalization from this conclusion is, however, no more justifiable than is that so often made from observations which seem to point in the opposite direction. It does not seem probable that uniformity exists here any more than in other features of development in regard to which premature generalizations mark like wrecks the dangers along the channel of biological thought.

In slightly later stages it is difficult or impossible to determine with certainty which testes have arisen from the smaller and which from the larger cells. Figs. 3, *A*–3, *F* (Pl. VII.), represent young testes which probably developed from the smaller parenchymal nuclei: amitosis is visible in all cases except Fig. 3, *F*, in which mitosis is occurring. In the hundreds of testes examined at this stage four cases of mitotic division have been observed of which one is shown in this figure. All of the observed cases were found in a single chain of *Moniezia expansa*, another fact which seems to indicate that the relative frequency of the two forms of division may vary. It was not possible to determine the number of chromosomes with certainty, but it was more than twelve, the number shown in the figure.

Figs. 4, *A*–4, *D* (Pl. VIII.), represent cases which probably developed from the large cells — muscle cells. Such stages are found in the same proglottids as the stages shown in Figs. 3, *A*–*F*, and are clearly larger and contain more nuclei than the latter. Fig. 4, *A*, shows a case in which a small nucleus, apparently not a part of the large mass, is also seemingly involved in the development. Cases of this sort are not infrequent, and the small nucleus often becomes one of the membrane-nuclei, though the latter appear in many cases to arise from the same primordium as the germ-cells themselves. Here, as in the development of the female organs, it is difficult to resist the impression that the development of these organs is the result of some localized stimulus or condition and that any cells within reach of this factor may become involved.

At this stage the nuclei of the developing testis lie in a con-

tinuous mass of cytoplasm, which is more or less distinctly marked off from the parenchymal substance, but still shows fibrous extensions into the parenchyma. The development of the testes differs from that of the ovary in that none of the parenchymal substance is included within the testis. This difference is merely the consequence of the fact that the testes usually develop from a single nucleus and its surrounding cytoplasm, while the ovary develops from a large number of the parenchymal nuclei.

II. *The Growth of the Testes Preceding the Spireme Stage.*

During the period preceding the appearance of the spireme in a part of the cells the development of the testes consists of increase in size as the result of numerous divisions, chiefly amitotic and of formation of the membrane about the testis and of the vasa efferentia.

The formation of the membrane occurs at an early stage from the cytoplasm of cells about the periphery of the proliferating mass. Fig. 5, *A* (Pl. VIII.), shows one of these cells with the membrane forming an extension of the cytoplasm. The vas efferens is formed in the same manner (Fig. 6, *A*, Pl. VIII.). The membrane-forming cells are few in number and the nuclei apparently undergo degeneration in later stages, for they are very rarely found in the fully developed testis.

The contents differ somewhat in appearance according to the method of fixation employed. After Hermann or chrom-oxalic the nuclei appear in most cases to be imbedded in a syncytial mass of cytoplasm, cell boundaries being indistinguishable or sometimes faintly visible, though cavities or vacuoles are frequently observed. After sublimate and some of the sublimate mixtures in all but the earlier stages the cytoplasm appears to have undergone shrinkage and to be more or less definitely concentrated about each of the nuclei. In later stages the individual cells appear more distinct after any fluids. The earliest stages of testis-development are certainly syncytial and without doubt the individualization of the cells takes place gradually. In consequence of the shrinkage of the delicate and probably highly fluid protoplasm caused by the sublimate fluids the distinctness of the cells is exaggerated. Most of the figures of these stages (Figs. 5,

A–6, *B*, Pl. VIII., 7, *A*–8, *B*, Pl. IX.) are taken from the chrom-oxalic preparations and cell-boundaries do not appear in most cases though they may be present. Fig. 9, *D* (Pl. IX.) is taken from a sublimate preparation at a rather late prespireme stage and shows the cells as distinct.

But for present purposes the nuclei are of chief importance. Figs. 5, *A*–5, *C* (Pl. VIII.) represent stages just after the formation of the membrane. In Figs. 5, *A*, and 5, *B*, amitoses are visible and in Figs. 5, *B*, and 5, *C*, two of the very infrequent cases of mitosis in these stages are shown. Figs. 6, *A*, and 6, *B* (Pl. VIII.) are from slightly later stages: Fig. 6, *A*, is a section through one side of a testis and does not show the full size. Both figures show amitoses and Fig. 6, *B*, shows one case of mitosis. Figs. 7, *A*, and 7, *B* (Pl. IX.), are from still later stages. In the latter figure one case of division of a nucleus into three parts is shown. The nuclei in which such divisions take place are usually larger than the others, often lie near the center of the testes and are similar in appearance to the large nuclei along the axis of the developing ovarian follicles which were mentioned in the preceding paper. In Figs. 8, *A*, and 8, *B* (Pl. IX.), stages just preceding the first appearance of the spireme, each with several amitoses, are shown. In Fig. 8, *A*, one of the large nuclei dividing into three parts is seen near the opening of the vas efferens.

In Fig. 9, *A*–9, *D* (Pl. IX.), cells or cell-groups from various stages containing amitoses of special interest are shown. Figs. 9, *A*, and 9, *C*, represent cases of the form of amitosis designated endogenous in the preceding paper in which the two nuclei resulting from division do not occupy the entire space within the old membrane. Numerous cases of this sort have been observed in the testes and have been examined with great care. Fig. 9, *B*, is a case of triple division and Fig. 9, *D*, a case of cytoplasmic division proceeding from within outward. This figure is from a sublimate preparation.

During these stages mitoses are rare. Very often not a single case is found in any of the numerous testes of a proglottid. In other proglottids a number of testes may show one or more each. In general the relative frequency of mitosis appears to vary in

different chains and in different proglottids. In one chain of *M. planissima* for example mitosis has been observed only very rarely though the chain has been carefully examined; in another it was found to be much more frequent. In all cases, however, amitosis is the predominant form of division in these stages.

III. *Formation of the Spireme and the Growth Period.*

In the stages before spireme-formation, or as it has often been called, synapsis, all the nuclei in the testes are similar in appearance and contain a large deeply staining nucleolus with perhaps a few smaller granules.

Suddenly a part of the nuclei begin to increase in size and a spireme appears (Figs. 10, *A*–13, *B*, Pl. X.). The formation of the spireme takes place in the manner described for the ovary in the preceding paper of this series. The change does not appear to begin in any particular region of the testis. Sometimes different groups of cells in different regions of the same testis give rise to a spireme while about them and between them lie others still unchanged and undergoing amitosis. From the first appearance of the spireme in the testes until the formation of spermatozoa is completed the multiplication of the spermatogonia which remain in the prespireme stage goes on, chiefly or wholly by amitosis and some of the cells thus produced are continually passing into the spireme stage. Consequently the stage is not characteristic of any particular period of development of the testis as a whole after its first appearance; in the older testes some groups of cells in the spireme stage and some groups of spermatogonia in prespireme stages are always to be found.

In some testes before the spireme stage appears and frequently afterward some of the cells are seen to be more or less pear-shaped in form with the pointed ends radially arranged about a center and united by strands of cytoplasm (Figs. 10, *A*, 11, *B*, Pl. X.). The number of cells in a group of this kind varies from three or four to eight or ten. All the cells of a group pass into the spireme stage simultaneously. Whether such groups are due to the persistence of cytoplasmic connections from previous divisions or to the formation of new connections it has been impossible to determine, but it seems possible from the varying size of

the groups that they are merely the result of connection of cells lying near each other.

The grouping of the cells is not by any means a characteristic feature in these stages. Frequently cells which are entirely separate from each other pass into the spireme stage simultaneously (Figs. 10, *B*, 11, *A*, Pl. X.). As will appear below, the grouping is merely the first step in a process characteristic of spermatogenesis and observation indicates that in some cells it begins before the spireme appears in others not until later.

As in the ovary the spireme is usually massed at one side of the nucleus as in many other cases of synapsis and is often visibly connected with the nucleolus (Figs. 12, *A*–12 *B*, Pl. X.), which, however, does not decrease in size but increases as the nucleus grows larger (Figs. 10, *A*–13, *B*, Pl. X.).

The appearance of the spireme is accompanied by an increase in the amount of cytoplasm. Comparison of the cells in this stage with those in earlier stages in Figs. 10, *A*, 10, *B*, and 11, A (Pl. X.), shows this difference clearly. The cytoplasm in the spireme stages also appears somewhat more dense in structure and stains a little more deeply. Here as in the ovary the apparent connection of the nuclear changes with the growth of the cytoplasm is most striking.

As is usual, this stage in the testes is not accompanied by such extreme growth of the cytoplasm as in the ovary nor by any formation of yolk, but is soon followed by the spermatogenetic divisions.

But the stages following the spireme are not the same in all cells; the later development follows two very different lines. In the later stages of the spireme period it is possible to distinguish two different sorts of nuclei. In the one (Fig. 13, *A*, Pl. X.) the nucleolus has disappeared and the spireme is very dense and occupies almost the whole periphery of the nucleus. Careful examination and comparison has convinced me that these nuclei are in preparation for the first spermatocytic mitosis. The nuclei of the other sort are considerably larger (Fig. 13, *B*, Pl. X.), the spireme is much less dense and more irregular in form and does not occupy the whole periphery but is still massed more or less at one side and the nucleolus is still intact. I am confident that

these nuclei do not represent earlier stages than those in Fig. 13, *A*, for they are always larger than the latter and the irregularity of the spireme is not found in the earlier stages. These nuclei are the first stages in a remarkable process of fragmentation which will be described in a later section. Their relative frequency as compared with the others appears to vary in different chains, proglottids and regions. Sometimes they seem to be more, sometimes less numerous than the others.

(To be continued.)

Explanation of Plates.

Plate VII.

Fig. 1. *A–D*, testes forming from parenchymal cells: amitotic division in all cases.

Fig. 2. *A*, muscle cell; *B*, muscle cell undergoing amitosis; *C*, *D*, *E*, muscle cells developing into testes; in *E* the muscle fiber is apparently undergoing degeneration.

Fig. 3. *A–F*, young testes; in *F* a case of mitosis.

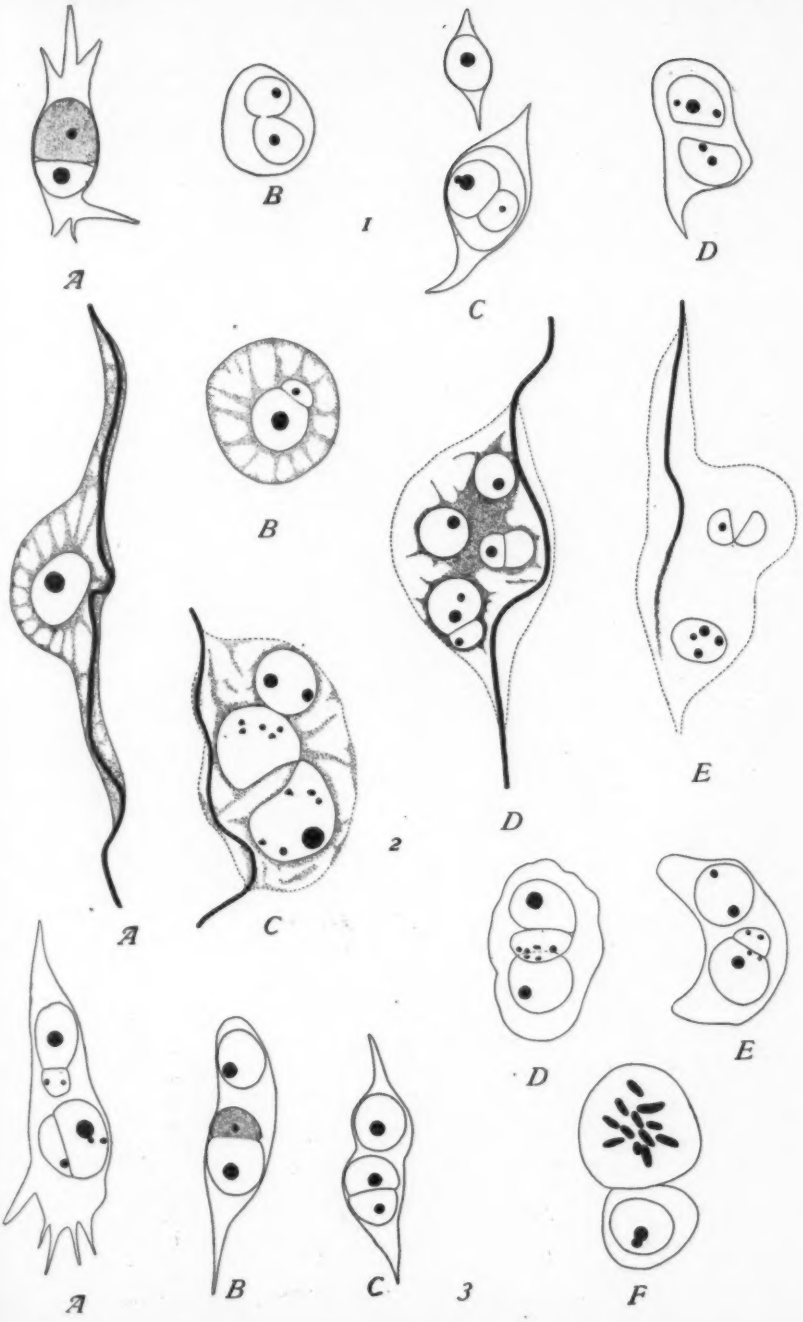
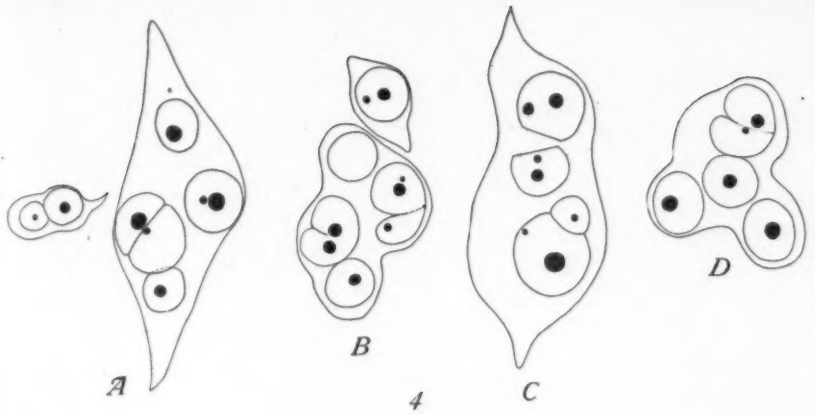

A
B
1
C
D
A
B
C
2
D
E
A
B
C
3
D
E
F

PLATE VIII.

FIG. 4. *A–D*, young testes showing amitosis.

FIG. 5. *A–C*, young testes after formation of membrane and vas efferens; *B* and *C* contain mitoses.

FIG. 6. *A*, *B*, developing testes.



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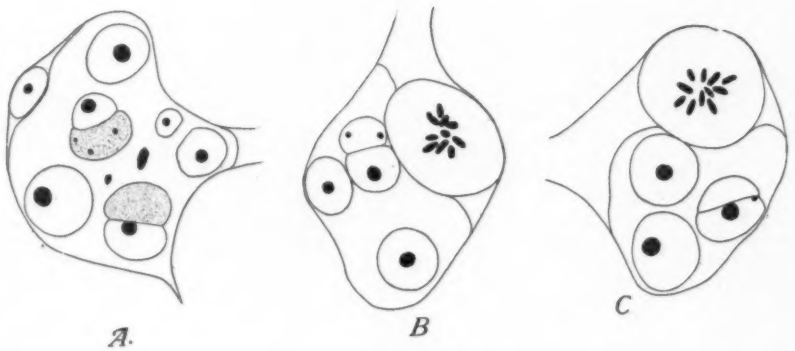

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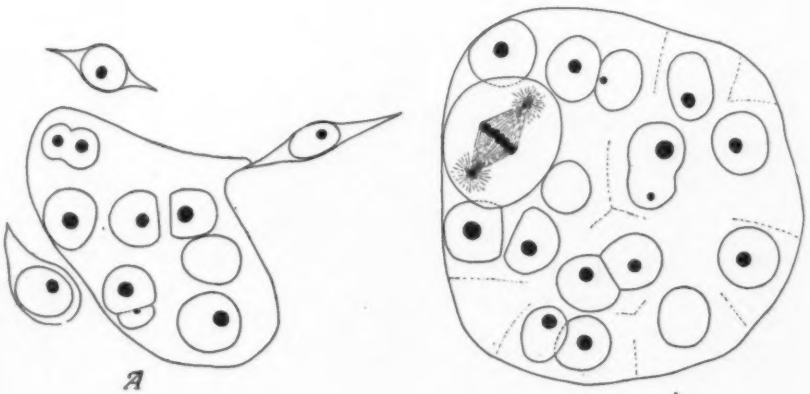

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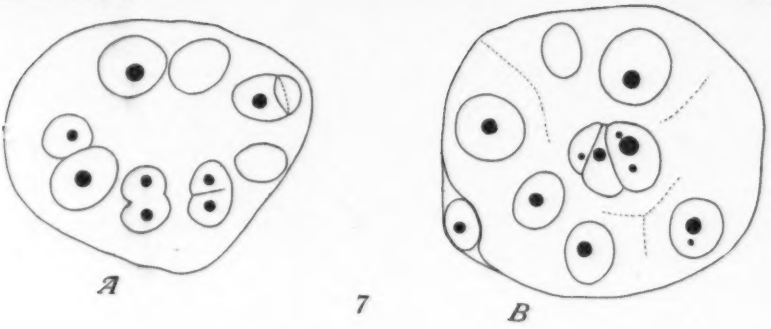
PLATE IX.

FIG. 7. *A*, *B*, developing testes.
FIG. 8. *A*, *B*, developing testes in later stages.
FIG. 9. *A–D*, amitoses from developing testes.



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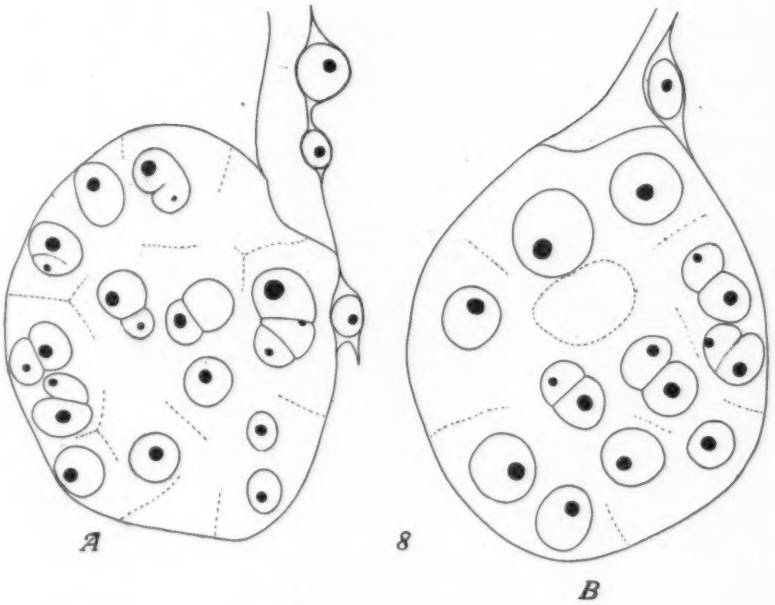

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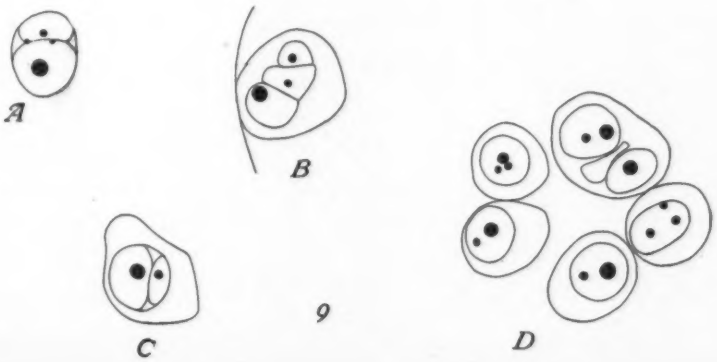

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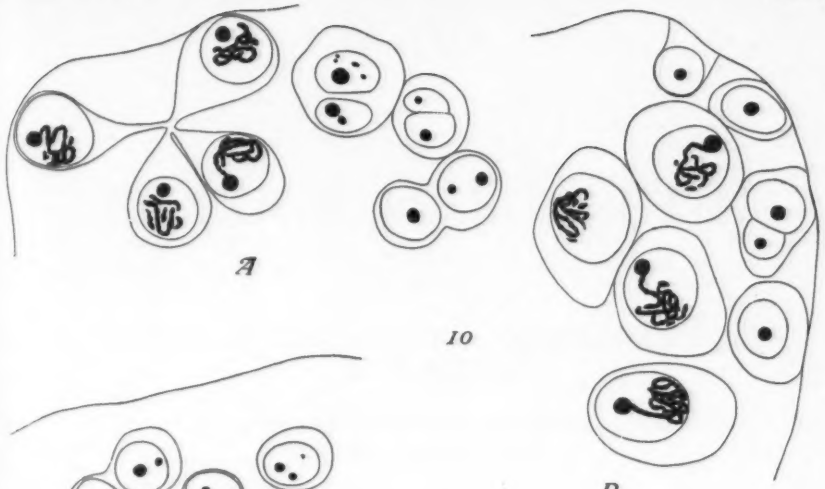
PLATE X.

FIG. 10. *A*, *B*, Fig. 11; *A*, *B*, the spireme stage. Figs. 10, *A*, and 11, B, show the first stages in fusion of the spermatocytes to form a cytophore.

FIG. 12. *A*, *B*, spireme stages.

FIG. 13. *A*, preparation for first spermatocytic mitosis; *B*, preparation for fragmentation.



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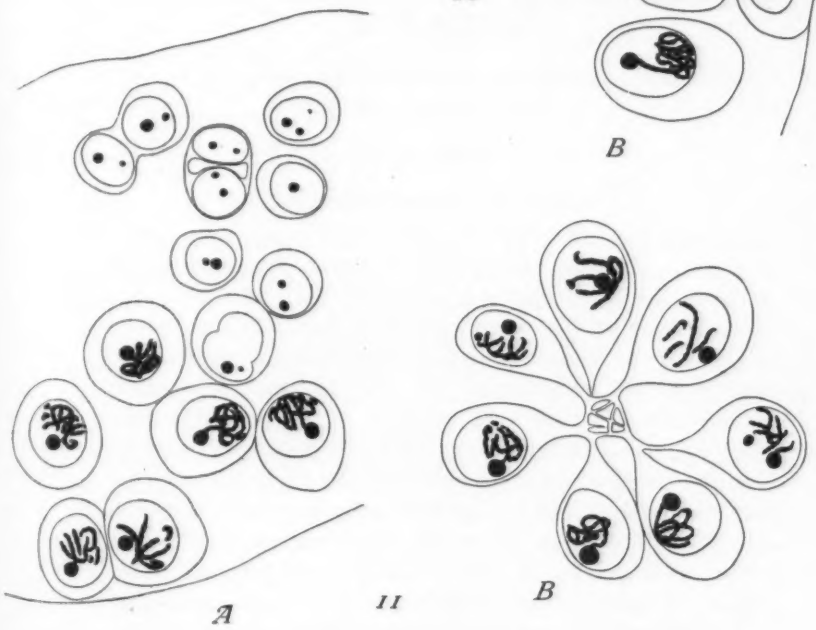

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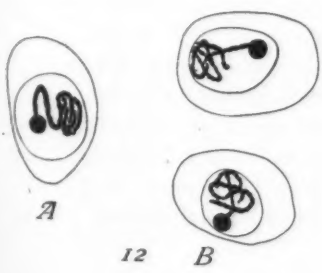

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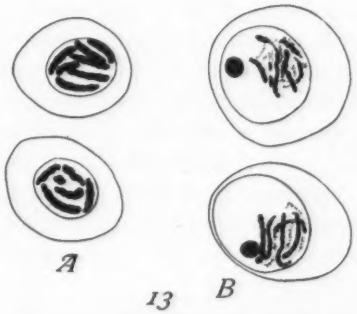

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